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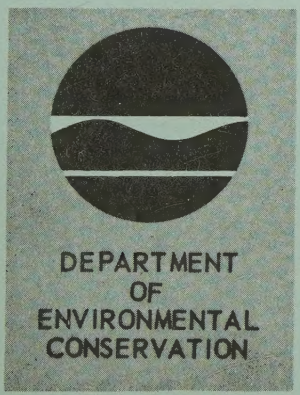

July, 1980

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NEW YORK FISH AND GAME JOURNAL

VOLUME 27 July, 1980 NUMBER 2

EVOLUTION OF A MANAGEMENT STRATEGY FOR THE WALLEYE IN ONEIDA LAKE, NEW YORK[1]

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ABSTRACT

The search for a viable management strategy for the walleye in Oneida Lake began in the 1950's when fluctuations in the catch and other symptoms of stress were first detected. Surveys to estimate the harvest and the abundance of stock established the fact that angling exploitation was intense in some years, but much of the variability in walleye abundance was attributable to 40-fold fluctuations in recruitment. Subsequent research focused on questions of how recruitment was regulated and interactions between the walleye and its primary prey the yellow perch.

Managers who expect large gains in yield by fine-tuning sport fisheries will find little encouragement in this paper. Frequent changes in the vulnerability of the walleye to angling reduced the effectiveness of angling regulations, and hopes of increasing recruitment were frustrated by evidence that there were few "surplus" prey to support a larger predator population.

Notes gleaned from journals of early travelers through western New York provide our earliest perception of the Oneida Lake fishery. Native Americans constructed elaborate rock weirs at the outlet of the lake to trap eels during their immigration, and numerous salmon were speared at the weirs and as they entered tributaries to spawn (Campbell, 1849). Early settlers had established a commercial salmon fishery by the turn of the 19th century, but this resource was quickly depleted (DeKay, 1942).

Cobb (1905) estimated that the commercial harvest was 22,777 kilograms in 1894 and 99,500 kilograms in 1895, excluding eels taken in weirs. Suckers, bullheads, walleyes, pickerel and yellow perch in descending order of importance contributed to the commercial catch. Conflicts between sport and commercial fishermen led to a ban on netting in 1897, but it is doubtful that the fisheries were seriously constrained. Sale of walleyes and most other species taken by hook and line was legal which facilitated the sale of those taken illegally. C. F. Davison, a fish dealer and former commercial fisherman, estimated that the total catch in 1928 was 226,000 to 272,000 kilograms, including both the sport and illegal com-

[1]Federal Aid in Fish and Wildlife Restoration funds through the New York State Department of Environmental Conservation and its predecessor the Department of Conservation (under Project F-17-R) have provided continuous support for fisheries studies on Oneida Lake for two decades. Numerous colleagues and students contributed to the study and many of their names appear in the Literature Cited.

mercial catch (Adams and Hankinson, 1928). Although the harvest was pursued vigorously and with few restrictions, the only species extirpated was the migrant salmon which declined throughout the Lake Ontario basin.

Meanwhile cultural activities destined to profoundly change the fish community were taking place. Completion of the Barge Canal in 1916 opened a shipping route from the eastern seaboard to the Great Lakes (Barber, 1963), but dams and locks were barriers to the movement of fish between Oneida Lake and Lake Ontario. Water levels were stabilized to the benefit of riparian property owners and the detriment of northern pike and pickerel which spawned in flooded marshes. Stabilization of water levels promoted extensive urbanization of the shoreline (Greeson, 1971), which further degraded lowlands near the lake that were potential spawning grounds. Esocid spawning grounds were further diminished by the draining of marshes and expansion of truck farming.

Whether dams and locks were an effective barrier to the migration of elvers from Lake Ontario is unknown, but the catch of eels declined after completion of the canal and the fishery was abandoned about 20 years later. Equally dramatic was the demise of esocids, the importance of which can be inferred from descriptive accounts of the early fishery (Cobb, 1905; Adams and Hankinson, 1928; Van Cleave and Mueller, 1934). Walleyes and pickerel were about equally abundant while northern pike were common but less abundant. However, by the winter of 1945-46 when the State Conservation Department conducted a postcard survey, the reported catch was 5,032 walleyes and only 127 esocids. In recent years northern pike have remained scarce and the pickerel population has approached extinction.

The loss of eels and esocids failed to stimulate any recorded public concern or scientific inquiry. The eel fishery was small and probably had little political clout, but the pickerel must have had many adherents. Angry outcries of pickerel fishermen may have been muted by an increase in walleyes that probably paralleled the decline in esocids (Forney, 1977b). Anglers' perception of the fishery may have also been influenced by a substabcial increase in the average size of yellow perch which enhanced their recreational value.

By the 1940's the walleye was clearly the predominant predator with the smallmouth bass a distant second. Notes, memos and unpublished reports (Burdick and Lipschuetz, 1946; Stone and Pasko, 1946) from the files of the State Conservation Department suggest that the principal public concerns of the period were environmental. Blooms of blue-green algae were severe enough to cause several fish kills when light winds concentrated the algae in bays. There was also public awareness that vast beds of emergent plants which rimmed the lake in earlier years (Baker, 1916, 1918; Adams and Hankinson, 1928) had disappeared. Winter draw-down of the lake was a popular but unverified explanation for the sparse aquatic vegeta-

tion. Despite symptoms of ecological stress at lower trophic levels the walleye seemed to prosper. The catch of walleyes in nets operated by the Oneida State Fish Hatchery was increasing, young walleyes were abundant and growth of older walleyes was slow which was interpreted as evidence of high population density (Stone and Pasko, 1946). These observations seemed to justify a creel limit of 15 walleyes, the use of up to 15 tip-ups, the sale of walleyes and other liberal regulations that were holdovers from the days of commercial fishing.

The first hint that all was not well were reports of poor walleye fishing in the early 1950's. More disturbing was the appearance of several exotics. The white perch probably invaded the lake from the Mohawk-Hudson River system via the Barge Canal (Scott and Christie, 1963), and a strong year class developed in 1952. Two years later vast schools of young gizzard shad appeared along the shore, and the native lake emerald shiner which had for decades supported a large bait fishery became commercially extinct.

These events stimulated new interest in the biology of the walleye (*Stizostedion vitreum vitreum*) in Oneida Lake which would eventually culminate in a long-term research commitment. Walleyes taken in nets set by the Oneida hatchery were tagged in 1952, beginning an annual ritual that was to continue for over a decade. The rationale for tagging was never stated, but tag returns did confirm what fishermen already knew—that angling success was oscillating violently. While no one could explain why the catch was varying, pessimists noted that violent fluctuations in catch often preceded the collapse of a population. This dire prospect, together with a general feeling that more information was needed, led the State Conservation Department to contract with the Department of Conservation at Cornell University to explain the recent changes. Supported by State and Federal Aid funds, the first of a long series of fishery studies was begun in 1957.

PHASE ONE—SURVEY AND INVENTORY

The effect of fishing on walleye stocks was of most immediate concern to managers, and the need to evaluate exploitation dictated the initial direction of research. Some fishermen, particularly those who could trace their lineage to the days of commercial fishing, doubted that a few hundred or even thousand hooks dangling in a 20,700-hectare lake could deplete the supply of fish. Speculation about the role of angling in the population dynamics of the walleye could be most convincingly laid to rest by simultaneously measuring the catch and abundance of walleyes. Techniques of resource assessment by censusing fishermen and fish had reached a fair degree of sophistication by the 1950's, but their use had generally been restricted to small bodies of water.

In their pursuit of the walleye, anglers fished day and night, on water

and ice, from May 1 to March 1. To derive reasonably accurate estimates of fishermen and man hours of fishing effort, frequent counts of boats in summer and fishermen in winter were made from a 70-foot tower. Simultaneous airplane and tower counts established the proportion of the boats on the lake that were visible from the tower under a range of weather conditions. At night each boat deployed a gas lantern to attract lake emerald shiners which in turn supposedly attracted walleyes. Although few lake emerald shiners were seen in the late 1950's, continuation of the long-standing practice facilitated counting boats at night.

Roving census clerks interviewed fishermen to determine the number of fish caught which was the other ingredient needed to estimate the annual catch of walleyes. Grosslein (1961) analyzed the mass of statistical information and determined fishing effort and harvest for the period 1957-1960. As expected, most fishing effort was concentrated in summer with only modest year to year variation (Table 1). More dramatic were the annual

Table 1. Estimated Man-hours of Fishing on Oneida Lake During the Summer and Winter Seasons in 1957-58, 1958-59 and 1959-60*

	Man-hours of fishing§			
			Total	
Year	Summer	Winter	Number	Per acre
1957-58	804,000	37,000	841,000	17
1958-59	665,000	108,000	773,000	15
1959-60	1,216,000	96,000	1,312,000	26

*The summer season extends from May 1 to October 31; fishing effort from November 1 to the time of ice formation is negligible. The winter season extends from the time of ice formation to March 1.

§For the summer, estimates of the total boat-hours of actual fishing time during daylight hours were multiplied by 1.13 to obtain estimates of the total boat-hours of time spent on the lake, i.e., including time spent traveling between fishing sites, etc. The factor 1.13 was determined from the ratios of moving to non-moving boats observed during the boat counts to assess fishing effort. Total boat-hours of night fishing were added to the adjusted total for daylight hours and the grand total was multiplied by 2, the approximate average number of anglers per boat, to obtain estimates of total man-hours. In the winter, fishing effort was estimated directly in terms of man-hours spent on the lake.

fluctuations in the walleye harvest with the best year contributing 10 times that of the poorest (Table 2). Yellow perch helped sustain the fishery in years when few walleyes were landed, but the walleye was the prime target.

While information on the catch was accumulating, other studies were aimed at measuring the number of walleyes available to the fishery. The approach was to fin clip and release fish taken on the spawning grounds and to estimate the population from the ratio of marked to unmarked walleyes observed in samples collected during the post-spawning period. The Oneida hatchery routinely set trapnets near the mouth of Scriba Creek to intercept spawning walleyes, and 10,000 to 20,000 were processed for eggs. Fish spawning in 1957 were the first recipients of a distinctive fin

TABLE 2. ESTIMATED ANGLER CATCH OF WALLEYES, SMALLMOUTH BASS, YELLOW PERCH AND ALL SPECIES COMBINED ON ONEIDA LAKE DURING THE SUMMER AND WINTER SEASONS IN 1957-58, 1958-59 AND 1959-60

Year	Species	Catch					
		Summer		Winter		Total	
		Number	Per cent*	Number	Per cent*	Number	Per cent*
1957-58	Walleye	36,000	9	4,000	27	40,000	10
	Smallmouth bass	17,000	4	. .	. .	17,000	4
	Yellow perch	247,000	63	10,000	67	257,000	63
	All species	393,000	100	15,000	100	408,000	100
1958-59	Walleye	55,000	21	57,000	65	112,000	32
	Smallmouth bass	18,000	7	. .	. .	18,000	5
	Yellow perch	114,000	44	27,000	31	141,000	41
	All species	259,000	100	88,000	100	347,000	100
1959-60	Walleye	413,000	57	50,000	53	463,000	56
	Smallmouth bass	31,000	4	. .	. .	31,000	4
	Yellow perch	160,000	22	36,000	38	196,000	24
	All species	724,000	100	95,000	100	819,000	100

*Of all species in each year, but the values for the three species listed total less than 100 because other fish are included under "all species".

clip (Eipper and Forney, 1965), and 89 of these were later observed in the angling catch and in samples taken in gillnets and trapnets (Forney, 1967). In later years electrofishing along the shore and trawling in deeper water provided larger recapture samples and presumably more precise estimates of the spring population.

The accuracy of population estimates rested on the assumption that marked fish behaved like unmarked fish, experienced the same mortality and were equally vulnerable to recapture (Ricker, 1975). The Scriba Creek spawning concentration was only one of several spawning groups, and evidence pointed to subtle differences in post-spawning distribution which could affect the proportion of marked to unmarked walleyes in recapture samples. Recoveries of fish tagged in several spawning runs showed that spawning populations intermingled during the summer, but a disproportional number of walleyes remained near their spawning grounds (Forney, 1963). To dispel any doubts about the accuracy of population estimates based on walleyes marked at Scriba Creek, independent estimates of the population were made in 1958-1960.

Walleyes captured in the fall, mostly by electrofishing, were fin clipped and subsamples were taken to determine the age, sex and maturity of those marked. Fall populations of age III and older walleyes were estimated from recoveries of marked fish in spawning runs in Scriba Creek and Fish Creek and near Dutchman's Island during the following spring. These estimates were adjusted for overwinter mortality and compared with population estimates of age IV and older walleyes in the spring. The in-

TABLE 3. POPULATION OF AGE IV AND OLDER WALLEYES IN APRIL AS PROJECTED FROM FALL ESTIMATES OF AGE III AND OLDER FISH IN OCTOBER AND AS CALCULATED FROM WALLEYES MARKED IN THE SPAWNING RUN

Year	Population in April	
	Projected from fall estimates	Calculated from spawning runs
1959	840,000	961,000
1960	430,000	504,000
1961	760,000	840,000

stantaneous natural mortality rate from November was about 3 per cent and the angling catch was approximately 57,000 in the winter of 1958-59, 50,000 in 1959-60 and 15,000 in 1960-61 (Forney, 1967). Spring populations projected from fall estimates were slightly lower than estimates of the April population calculated from fish marked in the spawning run (Table 3). However, agreement was sufficiently close to confirm that the procedure for estimating the spring population was valid.

Comparison of population estimates and creel census statistics dispelled any lingering doubts about the efficiency of the fishermen (Figure 1). The

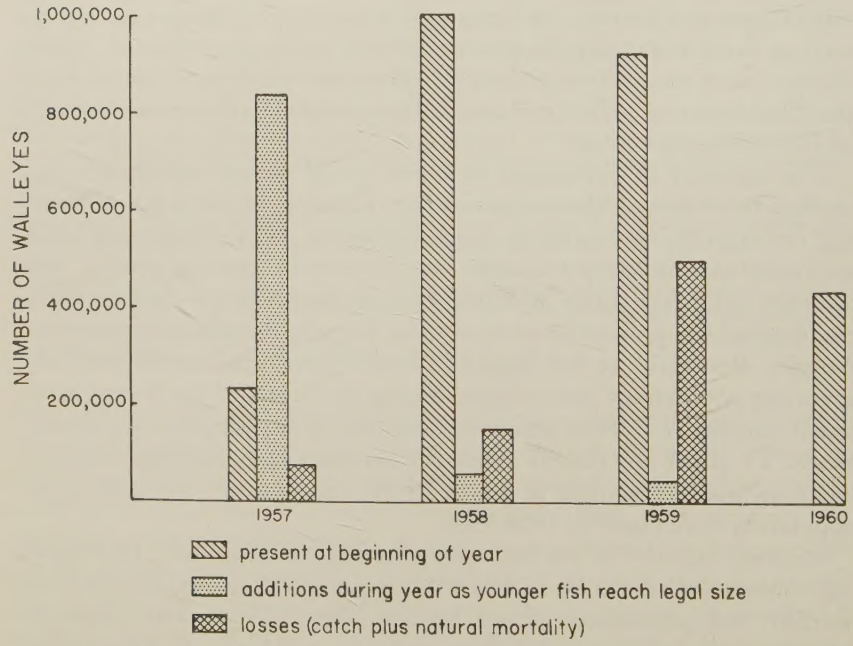

Figure 1. Number of legal-sized walleyes present in Oneida Lake at the beginning of the year from 1957 to 1960, together with the number reaching legal size during the year and the number of legal-sized walleyes removed from the population in 1957, 1958 and 1959. Annual additions represent the 1954, 1955 and 1956 year classes for the three years, respectively.

low spring population of 266,000 in 1957 followed a year in which fishing success was high. A preliminary census in 1956 (unpublished) indicated a minimum catch of 250,000 walleyes which approached the number remaining in the spring of 1957. Between April 1957 and April 1958, the population rose to 1,035,000, then declined slightly to 961,000 in the spring of 1959. The catch of 468,000 walleyes in 1959 caused an abrupt decline in the population to 504,000 in the spring of 1960.

Although the angling catch could determine the size of the walleye population, the number of walleyes available did not necessarily determine the number caught. There were about the same numbers of walleyes in 1958 and 1959, but fishermen landed 55,000 in 1958 and 413,000 in 1959. Fishing in terms of man hours required to catch walleye was five times better in 1959.

Changes in the vulnerability of walleyes to angling probably resulted from fluctuations in food abundance. Rates of exploitation as indicated by voluntary tag returns were high in 1953, 1956 and 1959, and these were years in which annual growth increments of age IV to VI walleyes were minimal (Figure 2). The conclusion that well-fed, rapidly growing walleyes were harder to catch than hungry walleyes would come as no surprise to fishermen, but the observation did have important management implications. Removal of a large number of walleyes in one year would be expected to increase the food supply of those remaining and result in good growth and poor fishing the following year. There would be little danger of overexploiting walleyes by angling if populations were only vulnerable when at or near the carrying capacity (Moyle, 1949). The pattern of a year of high exploitation followed by a year or two of rapid walleye growth in

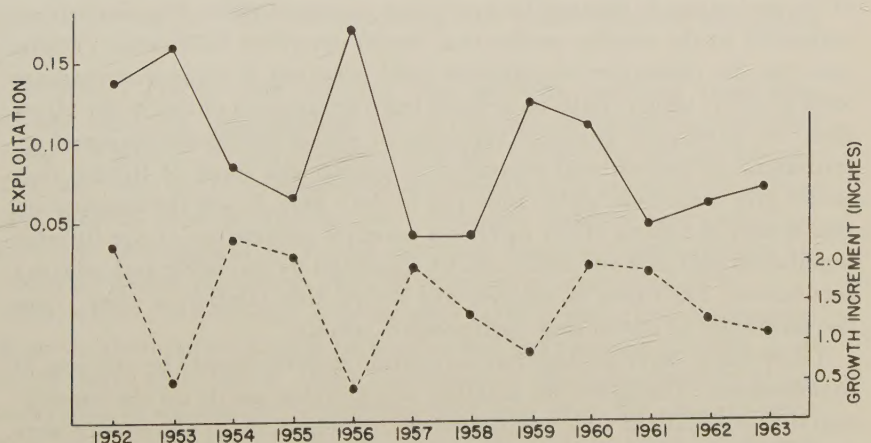

Figure 2. Mean growth increments for age IV to VI walleyes (dash line) and minimum rates of exploitation, i.e., ratio of number harvested to initial number, based on tag returns (solid line), 1952-1963.

the 1950's (Figure 2) supported the idea that angling only took the surplus and that liberal regulations were probably justified. While the interpretation seemed logical, subsequent observations would show that the postulated feed-back mechanism was less effective than hypothesized and that unrestricted angling could seriously deplete the walleye population.

The number of walleyes recruited to the adult stock and the number harvested explained most of the observed changes in adult stock. For example, the number of age IV and older walleyes decreased by 452,000 between 1959 and 1960. Subtracting the 449,000 age IV and older fish which were harvested and adding 37,000 walleyes recruited to the population between 1959 and 1960 left only 40,000 unaccounted for. "Natural" deaths in other years were equally low, and a more detailed analysis of recoveries of marked fish suggested that natural mortality rates were approximately 6 per cent (Forney, 1967). This meant that at prevailing rates of exploitation about 80 out of every 100 walleyes recruited to the adult stock would eventually be caught by anglers.

Evidence that the supply of walleyes was not inexhaustable increased public opposition to the commercial sale of walleyes caught by hook and line. It could be argued that "commercial" fishermen were in competition with recreational anglers because most walleyes that reached catchable size would eventually be harvested. Sale of walleyes caught in Oneida Lake was banned in 1960 ending the last vestige of the early commercial fishery. What proportion of the catch had been sold was unknown and the effect of the ban on the fishery would remain obscure. However, the restriction on commercial sale strengthened the prevailing enthusiasm for conservation and scientific management.

Research had generated some useful observations but not enough information to define a practical management goal. The prevailing philosophy of the period was to manage for maximum sustained yield. The concept, as embodied in the surplus production model described by Shaefer (1954), was that the maximum equilibrium yield occurred at some intermediate level of effort which could be defined from an analysis of catch-per-effort data. An alternative approach espoused by Ricker (1975) incorporated information on growth and mortality to predict the force of fishing that would give maximum yield. Inherent in both models was the assumption that a unit of fishing effort catches a constant proportion of the fishable population and that the catch can be regulated by imposing and relaxing regulations. The catch of walleyes had shown little relation to effort, thus the possibility of optimizing yield seemed remote.

There was a vague feeling that population stability should be one goal of management. The desire for stability was founded partly on the assumption that populations which exhibited wide fluctuations in abundance were more likely to collapse. Equally important was the realization that an unstable fishery had undesirable economic consequences and generated

social unrest and controversy. Erratic recruitment of walleyes had characterized the 1950's. The 1954 year class had contributed over 800,000 walleyes to the adult stock, while fewer than 60,000 of those hatched in 1955 and 1956 had survived to age IV. If a high constant recruitment could be maintained, the effect of variation in angling exploitation on the population would be minimized, or so it seemed. The question of how walleye recruitment was regulated became the new focus of research.

PHASE TWO – RECRUITMENT

Scientists generally agreed that year-class size was established in the first year of life, but how or when was a mystery. Evidence that mortality was high during the egg and larval period, particularly in marine species, led many biologists to view the earliest stages of development as "critical" in the formation of year classes. Discovery of significant correlations between environmental conditions during the period of egg and larval development and the size of year classes recruited to the adult stock reinforced the idea that year-class size was fixed in the first few weeks of life. However, few correlations stood the test of time, and one could only speculate on the number of non-significant correlations that had been relegated to the files as unworthy of publication.

Tracing the progression of walleye year classes through sequential stages of development seemed to offer the best possibility of isolating the factor or factors regulating recruitment. Abundance of cohorts at the egg-larva-fingerling stage could be compared with the contribution of the year class to the fishery to delineate the critical period of year-class formation. Comparison of the survival experienced by different cohorts from the egg-larval, larval-fingerling and fingerling-adult stages could reveal the controlling mechanisms. While the idea of measuring year-class abundance at intervals during early life was appealing, few tested sampling techniques existed.

Eschmeyer (1950) had reported that walleyes hatching from eggs spawned on shoals "disappeared" only to reappear along the shore of lakes several weeks later. It was suspected that the larvae were pelagic in open water, and tows with fine-mesh nets soon revealed the presence of walleyes in the limnetic zone of Oneida Lake. Although walleyes were easily captured, the development of a valid sampling design for estimating larval abundance would require six years of frustrating experimentation.

Nets, a meter in diameter, were adopted as the primary gear for measuring larval abundance. Larvae of marine fish were known to avoid slow-moving meter nets (Isaacs, 1965), but errors in estimating relative abundance could be minimized by sampling each year when fish were the same size or age. Preliminary studies in 1960 established the fact that walleye eggs spawned in the lake and in tributaries hatched about 5 days after those held at the Oneida hatchery. Within another 5 days all larvae were

Table 4. Numbers of Walleye Fry Taken in Meter Nets at 11 Stations on Five Days During May From 1961 to 1963 and an Analysis of Variance of Transformed (Log + 1) Catches

Year	Number taken according to station											Total
	1	2	3	4	5	6	7	8	9	10	11	
1961	3	0	0	3	4	8	14	51	2	81	104	270
1962	34	104	42	14	12	24	18	141	15	168	67	639
1963	29	17	49	17	36	55	42	310	12	97	29	693

Source of variance	Degrees of freedom	Mean square	*F*
Year	2	2.68350	19.14
Station	10	1.27100	9.06
Date	4	0.03052	0.22
Year x station	20	0.34450	2.46
Station x date	40	0.10416	0.74
Year x date	8	0.17001	1.21
Residual	80	0.14022	
Total	164		

pelagic and concentrated in the upper 3 meters of the water column. Initially most walleyes were in open water, but later aggregations appeared in bays.

Beginning in 1961, meter nets were towed at 2 miles per hour for 5 minutes five times during an 8-hour period beginning 8 days after larvae reared at the Oneida hatchery were stocked. At each station, samples were taken at 1, 3 and 5 meters and the catch was pooled. Although the number of walleyes caught was impressive, the analysis of three years' data was not encouraging (Table 4). Examination of station totals showed that the distribution of larvae was different each year. Catches were highest at Station 11 in 1961, at Station 10 in 1962 and at Station 8 in 1963. Analysis of variance, after log + 1 transformation of the catches, showed the expected high station x year interaction.

If years and stations were considered samples drawn from a larger population, the year x station variance could be used to test for differences between years and to set confidence intervals for transformed catches as follows:

Year	Mean log	Confidence interval (95 per cent)
1961	0.44309	0.60137 - 0.28481
1962	0.81536	0.97364 - 0.65708
1963	0.83522	0.99350 - 0.67694

The broad confidence intervals indicated that meter-net samples would not provide precise indices of larval abundance. With the same effort, precision of estimates would be substantially improved by increasing the number of stations from 11 to 55 and sampling each station once. This revised sampling design was initiated in 1964 while other sampling gear and alternative methods of estimating larval abundance were explored.

These surveys provided valuable information on the origin, distribution and behavior of larvae. The highest concentrations of newly hatched larvae were consistently found in the northwestern corner of the lake where hatchery-reared larvae were stocked, and few were taken over known spawning grounds. Within a week to 10 days most larvae were found to the east and south of the stocking area which suggested that many were of hatchery origin and that water currents generated by the prevailing northwesterly winds determined post-stocking distribution. The tendency for larvae to concentrate near the surface during both the day and night would favor transport by surface currents (Table 5). Measurements of water currents (Houde and Forney, 1970) and studies of the swimming ability of larvae (Houde, 1969) would eventually confirm that the wind pattern following stocking explained the annual variation in distribution of larval walleyes.

TABLE 5. NUMBERS OF WALLEYE LARVAE TAKEN IN METER NETS TOWED AT THREE DEPTHS, DURING DAY AND NIGHT, IN 1962 AND 1963

Depth (meters)	Number of larvae		
	Day	Night	Total
0.0-2.0	196	122	318
2.1-3.5	102	77	179
3.6-5.5	112	83	195
Total	410	282	692

Larvae did not continue to drift passively but became concentrated in bays along the south shore (Figure 3). Initial transport of larvae into the bays may have been facilitated by surface currents, and eddy patterns generated by the prevailing northwesterly winds probably aided in retaining the larvae (Houde, 1969). Changes in the vertical distribution of walleyes in response to surface turbulence may have enabled them to regulate their distribution under varied wind regimes (Noble, 1972a). Whether concentration of walleyes in bays enhanced or reduced larval survival was never clear (Noble, 1972b), but local aggregations in bays complicated the sampling problem.

While efforts to sample larval walleyes were mired in statistical variability, considerable progress had been made in measuring fingerling abundance. Beach seining to assess the abundance of young fish was a well established technique (Maloney and Johnson, 1957), and large numbers of young walleyes could be easily collected in Oneida Lake (Raney and Lachner, 1942). Catches generally peaked in early July when young walleyes were about 60 millimeters long, and seining was timed to coincide with the period of highest catch. A 60-foot bag seine was hauled at nine sites three times a week for five weeks beginning in late June, and the mean

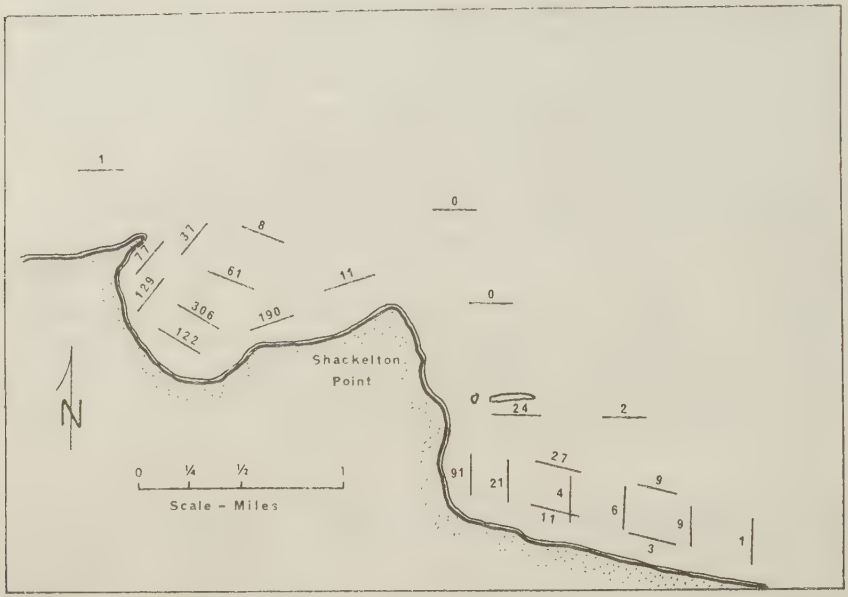

Figure 3. Numbers of young walleyes taken in meter nets towed for 5 minutes at depths of 1 and 3 meters in bays adjacent to Shackelton Point on May 24, 1963. Lines idicate course and length of tow.

catch per haul during the three consecutive weeks with the highest catches was used as an index of abundance.

Catches at the nine sites were low in 1960 and 1966 (Table 6). When the catches at individual sites in the seven years were ranked from lowest to highest, all the lowest and next to lowest values fell in 1960 or 1966. This

Table 6. Mean Catch Per Haul of Young Walleyes in Seines During June and July From 1960 to 1966 and Ranking of Year Classes at Individual Sites

	Mean catch at each station									Mean for all stations
Year	1	2	3	4	5	6	7	8	9	
1960	8	7	4	7	11	5	2	9	6	7
1961	57	63	37	125	88	58	28	60	121	71
1962	21	36	25	47	65	20	29	38	54	37
1963	65	82	55	79	32	46	37	90	52	60
1964	22	69	126	71	76	32	38	116	71	69
1965	59	40	24	75	34	22	11	30	31	36
1966	1	9	10	11	2	4	7	11	7	7
	Rank of year class at each station									
1960	2	1	1	1	2	2	1	1	1	xx
1961	5	5	5	7	7	7	4	5	7	xx
1962	3	3	4	3	5	3	5	4	5	xx
1963	7	7	6	6	3	6	6	6	4	xx
1964	4	6	7	4	6	5	7	7	6	xx
1965	6	4	3	5	4	4	3	3	3	xx
1966	1	2	2	2	1	1	2	2	2	xx

internal consistency indicated that exceptionally strong and weak year classes could be recognized from the catch in seines and that perhaps even finer distinctions were possible.

Not all young walleyes resided along the shore. Trawl catches revealed that they were scattered over the entire basin, although much of the bottom was muck and hardly fit the classical description of walleye habitat. At first, trawl samples were taken twice weekly in late summer to provide a check on the accuracy of seine catches as an index of year-class abundance (Table 7). Agreement was close considering that the seine catches were a

TABLE 7. COMPARISON OF CATCHES OF YOUNG WALLEYES IN SEINES AND IN TRAWLS DURING JUNE AND JULY FROM 1960 TO 1966

Year	Mean catch per haul	
	Seine (9 sites)	Trawl (4 sites)
1960	7	2
1961	71	12
1962	37	10
1963	60	14
1964	69	10
1965	36	9
1966	7	1

measure of abundance in early July while the trawl catches represented August-September. Mortality between these sampling periods could modify year-class abundance.

Indeed there was evidence from trawl catches that year-class abundance could change in late summer. The catch of young walleyes declined precipitously in some years while in other years it remained high through October (Figure 4). Apparently the period of year-class size formation was much longer than initially assumed and might even extend into the second year of life judging from the exponential decline in the catch of walleyes. Trawling operations were expanded from four sites to 10 and ultimately to 17 in an effort to define more precisely the time-space trajectory of cohorts.

Meanwhile the adaption of high-speed samplers, as described by Miller (1961), had achieved a breakthrough in the assessment of larval abundance. These small samplers with a 10-centimeter mouth could be towed for over 2 kilometers without clogging, and the long thin samples reduced the variance of catches by integrating the patchy distribution of walleyes. Miller samplers, when towed at 8 miles per hour, were much more efficient in capturing walleye and yellow perch larvae than the larger slow-moving meter nets (Noble, 1971), and the possibility of quantitative estimates of walleye larvae appeared promising.

Sampling became increasingly sophisticated with the advent of stratified random-sampling designs (Noble, 1968) and the development of size-dependent coefficients for adjusting catches for the avoidance of samplers

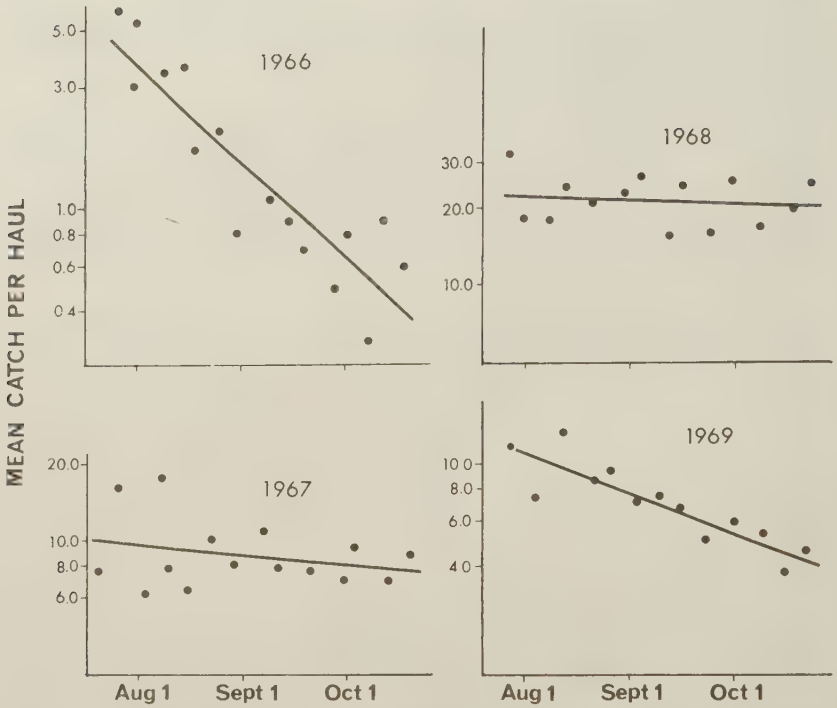

Figure 4. Mean catch of walleyes in trawls fished at 10 stations at approximately weekly intervals from July to October in 1966, 1967, 1968 and 1969.

by larval fish (Noble, 1970). With these advances, reasonably precise estimates of the number of walleye larvae were possible (Forney, 1975). These estimates confirmed what had been suspected from the pattern of larval distribution. Over two-thirds of the walleyes were of hatchery origin (Table 8). The substantial contribution of hatchery-reared larvae to the population indicated that few of the 12-18 billion eggs spawned annually survived. Most mortality between spawning and the time cohorts average 9 to 10 millimeters in length probably occurred during the embryonic period

Table 8. Number of Walleye Larvae Stocked and Estimated Population of Larvae in Oneida Lake 8-12 Days After Release, 1966-1973

Year	Number of larvae (millions)	
	Stocked	Estimated population
1966	194	32.8 ± 4.9
1967	157	21.9 ± 3.8
1968	180	40.5 ± 7.6
1969	0	10.2 ± 2.6
1970	310	48.4 ± 5.4
1971	0	6.6 ± 1.6
1972	214	29.2 ± 8.5
1973	0	8.2 ± 1.6

because few newly hatched larvae were taken over known spawning grounds or near the mouths of streams ascended by spawning walleyes.

As more year classes were followed through successive stages of development, it became apparent that high larval abundance did not guarantee a strong year class, nor was the number of fingerlings in late summer closely correlated with the number of walleyes recruited to the adult population (Table 9). The relative size of year classes frequently changed between the

TABLE 9. ABUNDANCE OF THE 1966 TO 1977 YEAR CLASSES OF WALLEYES AT INTERVALS FOLLOWING SPAWNING

Year class	Number of eggs (billions)	Larval population (millions)	Catch per effort in trawls			Number at age IV† (thousands)
			Age 0*		Age I§	
			Aug. 1	Oct. 15	(July-Oct.)	
1966	18	32.8	3.6	0.4	0.08	24
1967	14	21.9	9.6	7.9	0.72	198
1968	12	40.5	22.4	20.4	3.89	478
1969	15	10.2	10.8	4.6	0.03	12
1970	14	48.4	6.4	1.7	0.13	55
1971	12	6.6	4.5	3.6	3.40	640
1972	13	29.2	5.2	0.3	0.03	22
1973	12	8.2	0.2	0.1	0.14	40
1974	3	23.0	7.5	0.8	0.08	. .
1975	4	28.2	14.4	12.8	2.79	. .
1976	14	65.1	1.9	0.1	0.02	. .
1977	7	13.6	8.9	6.9	. .	. .
Coefficient of variation	0.39	0.64	0.76	1.26	1.49	1.32

*Predicted from regressions of mean weekly catches at 10 to 17 sites on time.
§Mean catch at 10 to 17 sites sampled at weekly intervals.
†Mark-recapture estimate of year-class abundance.

first and second years of life as shown by the catch of ages 0 and I walleyes in trawls. Evidence that the mean length of walleyes increased over winter at a time when growth was negligible suggested that losses might be caused by size-selective predation (Forney, 1966), but few young walleyes were observed in the stomachs of older walleyes.

The importance of cannibalism in regulating year-class size remained uncertain until 1969 when a concerted effort was made to examine walleye stomachs throughout the year (Chevalier, 1973). The number of young walleyes consumed by age II and older walleyes closely matched the decrease in the numbers caught in trawls between August and the following May (Table 10). Much of the overwinter mortality of young walleyes could be explained by predation, and the intensity of predation by older walleyes was probably governed by prey abundance. Catches of young walleyes in trawls had declined rapidly in 1966 and in 1969 (Figure 4) and in both years young perch were scarce in late summer. Later studies would reveal that young perch could buffer predation on young walleyes (Forney, 1974) and, as expected in a system where predation was intense, young walleyes that grew rapidly were more likely to survive (Forney, 1976a).

Table 10. Abundance of Young Walleyes on the First Day of the Month As Estimated From the Catch and Area Swept by Trawls, and the Number Consumed by Adult Walleyes, Between August 1969 and May 1970

Month	Abundance on first of month	Number consumed
August	2,177,000	1,053,000
September	1,535,000	1,005,000
October	1,094,000	192,000
November	771,000	215,000
December	550,000	
May	252,000	240,000*
Total	xxx	2,705,000

*Estimated for period from December 1, 1969 to May 1, 1970.

Studies had successfully described the distribution of early mortality and determined some of the variables controlling year-class abundance. The early concept that year-class size was established during a brief critical period in early life could be laid to rest. Losses during the egg and prolarval stage were high but remarkably stable. In three years when larvae were not stocked, mortality between the egg stage and the time the larvae were 9 to 10 millimeters long was 99.93 to 99.95 per cent. Mortality in other years must have been very near these values, otherwise, variation in the number of larvae originating from eggs spawned in the lake would have obscured the relationship between the abundance of larvae and the numbers stocked. Mortality between May when walleyes were pelagic and August when they were demersal was more variable, with 0.7 to 21.0 per cent surviving from the larval to fingerling stage. Fingerling density was based on the catch and area swept by trawls, and actual survival may have been higher if trawl catches underestimated the true density.

Despite early losses, fingerling density in August ranged from two to 318 per hectare, with numbers exceeding 18 per hectare in 16 of 17 years. Survival of 12 fingerlings per hectare to age IV would add 240,000 recruits to the adult stock which would roughly balance the annual mortality. Thus in most years the number of fingerlings in early summer was adequate to replenish the adult stock if conditions favored fingerling survival. Had walleye larvae not been routinely stocked, more year-class failures might have been traced to the larval stage. Fingerling density was only two per hectare in 1973 when the population was not augmented and consequently a weak year class was inevitable. Although the contribution of year classes to the adult stock reflected the accumulative effect of mortality at successive stages of development, cannibalism late in the first year of life could and often did establish year-class size.

The study of year-class formation had been launched with the expectation that research would reveal methods of increasing or at least stabilizing walleye recruitment. With the discovery that cannibalism regulated the survival of young walleyes, hope of increasing recruitment faded. Thus the

great leap forward by research left management about where it had been in the 1950's. However, evidence that cannibalism by older walleyes controlled recruitment did suggest that intense exploitation of walleyes entailed fewer risks than ititially assumed. Harvest of older walleyes would simply increase the survival of young walleyes, or so it seemed.

It was recognized that any reduction in the biomass of older walleyes that enhanced the survival of young walleyes would also benefit other prey. Young yellow perch were consumed in large numbers by walleyes, and the prospect of creating an overabundant, slow-growing population of perch as a by-product of an unrestricted walleye fishery was not appealing. If walleye predation regulated perch abundance, a minimum biomass of walleyes was needed to check the expansion of the perch population. Conversely, if perch and other prey populations were self-limited through intraspecific competition or predation, a *laissez-faire* fishery for walleyes held few dangers. These questions stimulated a final stanza in the search for a viable walleye management strategy.

PHASE THREE—PREDATOR-PREY RELATIONS

Examination of walleye stomachs and some simple arithmetic showed that walleyes consumed large numbers of prey and that, depending on the year, 60 to 95 per cent of the prey were young yellow perch. A rapid decline in the numbers of perch caught in trawls during late summer suggested that mortality was high, but the proportion of the mortality attributable to walleye predation was uncertain. Even less certain was the role of predation in population regulation. Although the literature on perch was voluminous (see Thorpe, 1977), how and when perch died in early life was a matter of speculation. Alm (1952) had shown that predation by older perch could suppress recruitment in small lakes where this was the only species, but most researchers had chosen to ignore the fact that young perch were prey and instead had searched for abiotic factors which might explain wide fluctuations in year-class abundance (Koonce et al., 1977).

Considerable information on yellow perch in Oneida Lake had accumulated as a by-product of walleye research. For every walleye caught a large number of perch were taken, and analysis of these catches revealed some elements of the life history. Perch moved inshore to spawn in late April as walleyes ceased spawning. There were localized spawning concentrations, and tagging indicated that adults returned to a home spawning ground in successive years (Clady, 1977). Post-spawning movements resulted in extensive intermixing of spawning groups which suggested that mark-recapture estimates of the adult stock were feasible.

Like the walleye, larval perch were pelagic and concentrated near the surface for several weeks after hatching. While walleye larvae became ag-

gregated in bays, perch were more abundant in open water which facilitated estimation of larval density. Transition to the demersal mode began in mid-June with the appearance of young along the shore, but most perch remained pelagic until they attained a length of 30 to 40 millimeters in July. Catches in trawls indicated a gradual movement of the population into deeper water during the summer with most young being found at depths of over 8 meters in October.

Two sorts of information could provide evidence that predation was important in regulating perch abundance. The role of predation might be documented by tracing the development of perch year classes and determining when and how year-class abundance was set. This approach had successfully identified factors limiting walleye abundance. A more direct approach was to measure the proportion of the young perch population that was consumed by walleyes. Studies of walleye-yellow perch interactions were developed along both lines.

To trace the development of perch year classes required estimates of year-class abundance at successive stages of development. Techniques for estimating the abundance of larval and fingerling perch from catches in high-speed samplers and trawls had already evolved. What remained was to determine how many eggs were spawned each year and how many of the fingerlings which survived the first year were recruited to the adult stock.

Buoyed by success in estimating the walleye population and bolstered by knowledge that nets set for walleyes by the Oneida hatchery often filled with yellow perch, the initial estimate of the perch population was made in 1969. Perch were remarkably vulnerable to capture in trapnets set during the spawning period. Over 45,000 were fin clipped in a 10-day period from six nets set near Shackelton Point and eight near Scriba Creek. Recaptures of these fish would show that about 2 per cent of the population had been captured in 140 net days. Over 80 per cent of the perch caught in trapnets in the spring were males, and most of these were age III and older.

Perch collected mostly in gillnets and trawls in summer and fall were examined for marks. Although there was some evidence from the distribution of recaptures that mixing of marked and unmarked fish was incomplete, ratios of marked to unmarked perch taken in different gear were in agreement (Table 11). This suggested that dispersal of fishing effort over most of the lake adequately compensated for incomplete mixing. Differences in vulnerability of males and females to capture were also a potential source of bias because a disproportionate number of the perch marked were males. However, a sex ratio of 1:1 for those taken in both gillnets and trawls implied that the sexes were equally vulnerable to capture during the post-spawning period.

The population was estimated by year class and it was obvious that recruitment was variable (Table 12). Age V perch comprised nearly half the adult stock in 1969 with most of the remaining fish being ages VI and

TABLE 11. RATIO OF MARKED TO UNMARKED YELLOW PERCH, AGE III AND OLDER, TAKEN IN VARIOUS GEAR DURING THE SUMMER IN 1969 AND 1977*

Gear	1969			1977		
	Catch	Recaptures	Ratio	Catch	Recaptures	Ratio
Gillnet	3,337	61	0.018	2,129	56	0.026
5.5-meter trawl	547	11	0.020	483	16	0.033
9.1-meter trawl	1,916	31	0.016	2,541	72	0.028
Electrofishing	. .	. .	. .	1,027	28	0.027

*Perch had been fin clipped on their spawning grounds in the spring.

TABLE 12. MARK-RECAPTURE ESTIMATE OF THE YELLOW PERCH POPULATION IN APRIL 1969 ACCORDING TO AGE

Age	Number marked	Recapture sample		Estimated population	Confidence interval (95 per cent)
		Total	Marked		
III	3,730	2,169	17	449,700	244,200 - 655,100
IV	2,336	773	11	150,700	67,700 - 233,600
V	24,676	4,326	94	1,123,900	897,000 - 1,350,800
VI	6,231	880	13	392,100	191,200 - 593,000
VII	7,050	631	13	318,300	155,700 - 480,800
VIII and over	1,599	184	3	74,000	8,527 - 139,400
Total	45,621	xxx	xx	2,690,400	2,259,100 - 3,121,800

VII. The predominance of older age groups suggested that angling exploitation was modest.

Grosslein (1961) estimated that anglers in 1957-1959 harvested about 200,000 perch annually. If a similar rate of harvest prevailed in 1969, anglers would have removed about 12 per cent of the adult stock. The total annual mortality determined from sequential mark-recapture estimates of the year classes from 1969 to 1977 was 35 per cent, indicating that angling might have accounted for about one-third of the deaths among older age groups. Substantial natural mortality was probably attributable to disease although the casual agent was never isolated. Observed deaths were concentrated from July through early August, and truckloads of perch were frequently removed from public beaches at the eastern end of the lake. Fish which succumbed exhibited red sores and open lesions, and most were age V and older. Deaths of adults from predation were probably infrequent. Perch generally attained a length of over 200 millimeters by age III, and few walleyes were capable of ingesting perch over 160 millimeters long (Nielsen, 1978).

Variation in recruitment caused fluctuations in the adult stock which were only partially dampened by the presence of older age groups (Figure 5). Recruitment of the strong 1970 year class to the adult stock boosted the population from less than 2 million in 1972 to over 4 million in 1973, but fewer than 200,000 recruits were added in the following two years and by 1975 the adult stock had slipped below 2 million. Estimates of recruitment and population abundance in even-numbered years were derived from

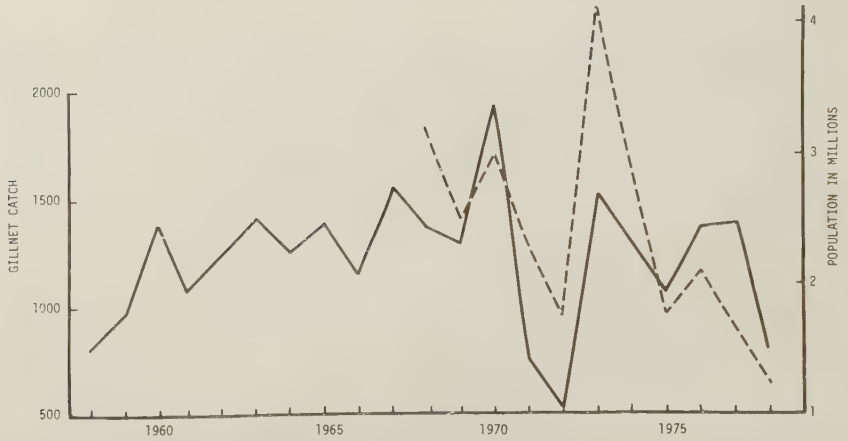

Figure 5. Total catch of age III and older yellow perch in 15 gillnet sets (solid line) made annually from 1958 to 1978 (except 1974) and mark-recapture estimates of the age III population (dash line).

mark-recapture estimates of year-class abundance in odd-numbered years and between-year survival rates. Trends in abundance determined from mark-recapture experiments were reflected in the catch of age III and older perch taken in gillnets set overnight at the same 15 sites annually (Figure 5). Abundance and age composition of stocks prior to 1969 were developed from the relationship between the total catch in gillnets and mark-recapture estimates for the years 1969 to 1975 with appropriate ad-

Table 13. Abundance* of Yellow Perch Year Classes in Oneida Lake at Several Life Stages, 1959-1977

Year class	Eggs (millions)	Age 0				Age III
		8 mm.	18 mm.	Aug. 1	Oct. 15	
1959	2.53	. .	. .	. .	. .	67
1960	2.47	. .	. .	. .	. .	46
1961	2.07	. .	. .	28,600	2,850	15
1962	2.24	. .	. .	21,100	4,350	53
1963	2.58	. .	. .	18,500	780	30
1964	2.60	. .	. .	26,000	4,990	97
1965	3.00	279,000	140,000	21,700	2,610	7
1966	2.68	121,000	40,000	12,000	150	22
1967	2.93	131,000	61,000	24,500	2,100	68
1968	3.02	. .	. .	36,000	6,700	8
1969	2.84	149,000	69,000	7,200	210	5
1970	2.83	200,000	69,000	14,000	900	144
1971	2.16	210,000	218,000	37,700	3,520	7
1972	2.63	143,000	110,000	2,500	100	1
1973	3.26	39,000	18,000	1,200	510	52
1974	3.28	77,000	30,000	3,100	320	13
1975	2.46	362,000	152,000	21,400	450	. .
1976	2.33	126,000	37,000	6,500	190	. .
1977	2.08	220,000	65,000	14,700	4,220	. .
Mean	2.62	172,000	83,000	17,400	2,050	40

*Number per hectare.

justments for the size selectivity of gillnets. These estimates of stock abundance suggested that recruitment was less variable and adult stock more stable in the 1960's than in the 1970's.

Although perch over age II outnumbered walleyes over age III about 3 to 1, differences in their biomass were much smaller. Perch biomass in the spring of 1969 was about 30 kilograms per hectare compared with 21 kilograms per hectare for walleyes. Since walleyes consumed only juvenile perch, a small biomass of adult perch could support a large predator population by producing many young (Kempinger and Carline, 1977). A substantial proportion of the adult perch production in Oneida Lake was devoted to reproduction. Production by age III and older perch in 1969 was 15.4 kilograms per hectare, and gonadal production was 40 per cent of the total (Vashro, 1975). The number of eggs produced in the spring of 1969 was about 2.84 million per hectare (284 per square meter) of lake surface. Egg production on other years fell within a fairly narrow range of 2.07 to 3.28 million per hectare (Table 13). Thus the initial size of year classes at the embryonic stage was similar in the period 1959 to 1977, and it was mortality at subsequent stages of development that was responsible for variation in cohort abundance.

Perch spawned at depths of 2 to 4 meters and the gelatinous strings of eggs were easily collected in small benthic sleds. Efforts to quantify egg abundance from these catches failed, but the samples did reveal information on egg distribution. Spawning was generally concentrated in semiprotected bays where the bottom was firm and covered with a sparse growth of macrophytes. Egg masses were rarely found at depths of less than 2 meters although the substrate appeared suitable. A high proportion of the eggs collected were viable and egg retention by female perch was seldom observed.

Of the 42 to 58 billion eggs spawned in 1969-1975 an average of 8 per cent produced larvae that survived long enough to be recruited to the pelagic population 3-4 weeks later (Clady, 1976a). Larval abundance was estimated from the catch in Miller samplers when cohorts averaged 8 millimeters long. Survival ranged from 1.6 to 18.4 per cent, and strong correlations were found between year-class survival, temperature and wind velocity during a 3-4 week period prior to the time cohorts attained a length of 8 millimeters. Inclusion of additional year classes and reanalysis of the 1969-1975 data supported these initial observations (Table 14). In a multiple linear regression, 65 per cent of the variability in survival of the 1965-1977 year classes could be "explained" by mean air temperature and wind velocity.

Temperature and wind may act synergistically to increase egg mortality. Dislodgement and destruction of eggs has been observed during periods of strong wave action (Clady and Hutchinson, 1975), and low temperatures would increase the risk of exposure to violent storms by prolonging incubation (Busch et al., 1975). Low water temperature could also adversely af-

Table 14. Survival of Yellow Perch From the Egg to the Date Pelagic Larvae Averaged 8 Millimeters Long, in Relation to Mean Daily Water and Air Temperatures During the Preceding Three Weeks and Mean Daily and Mean Daily Maximum Wind Velocity During the Preceding Four Weeks, 1965-1977

Year§	Survival from egg to larval length of 8 millimeters		Temperature (degrees Celsius)		Wind velocity† (kilometers per hour)	
	Per cent	Date	Water	Air†	Mean	Maximum
1965	9.3	May 26	. .	15.2	14.5	26.9
1966	4.5	June 4	. .	14.1	16.3	28.6
1967	4.4	June 2	. .	11.1	16.1	30.1
1969	5.2	May 24	11.4	12.6	13.5	30.4
1970	7.0	May 21	12.5	14.0	14.6	27.4
1971	9.7	June 1	11.8	14.6	14.0	26.5
1972	5.4	May 28	12.1	14.2	11.6	24.1
1973	1.2	May 25	11.0	10.6	15.0	27.5
1974	2.4	May 25	11.2	12.4	18.7	33.1
1975	14.7	May 24	11.5	16.4	12.9	25.6
1976	5.4	May 27	10.4	11.5	16.6	29.8
1977	10.6	May 21	11.9	13.1	15.4	28.0
Correlation coefficient, i.e., survival vs.:			0.55	0.76**	− 0.49	− 0.61*

§Data for 1968 lacking because survey was conducted before larvae were fully recruited to the pelagic mode.

†Records from U.S. Weather Bureau for Hancock Airport at Syracuse, N.Y. located 9 miles south of Oneida Lake.

*$P = < 0.05$

**$P = < 0.01$

fect the survival of newly hatched larvae (see Hokanson, 1977), but Clady (1976a) was unable to detect any evidence of catastrophic mortality during the period in which perch were recruited to the pelagic population. Although food abundance during early development is often cited as a critical factor in year-class formation, perch survival appeared insensitive to annual variation in zooplankton abundance and species composition (Clady, 1977).

Survival of perch from the egg stage to a length of 8 millimeters profoundly influenced the pattern of year-class development through the first year. Year classes which were abundant at the 8-millimeter size usually remained dominant through the summer while initially weak cohorts often approached extinction by fall (Table 13). Only modest changes in the ranking of cohorts occurred as pelagic perch grew from 8 to 18 millimeters, but after the young became demersal in mid-summer there was a marked divergence in relative abundance. The 1962, 1964 and 1968 cohorts which were abundant on August 1 experienced lower mortality than other year classes produced in the 1960's, and a 5-fold difference in relative abundance increased to a 40-fold difference by the end of the growing season. The most probable explanation for depensatory mortality (in contrast to compensatory) was predation, as discussed by Neave (1953) with respect to salmon. A stable biomass of walleyes would be expected to have consumed a larger proportion of the young perch in years when perch

TABLE 15. DENSITY AND BIOMASS OF YOUNG YELLOW PERCH ON AUGUST 1 AND INSTANTANEOUS MORTALITY COEFFICIENT FOR PERIOD OF JULY TO OCTOBER, TOGETHER WITH BIOMASS OF AGE III AND OLDER WALLEYES ON JULY 1, FOR THE YEARS 1961 TO 1977

Year	Yellow perch			Walleye biomass§ (kilograms per hectare)
	Density (number per hectare)	Biomass (kilograms per hectare)	Mortality coefficient*	
1961	28,600	19	0.030	21
1962	21,100	32	0.021	23
1963	18,500	21	0.042	25
1964	26,000	34	0.022	20
1965	21,700	17	0.028	23
1966	12,000	15	0.058	29
1967	24,500	33	0.033	21
1968	36,000	48	0.022	21
1969	7,200	9	0.047	22
1970	14,000	24	0.037	18
1971	37,700	26	0.031	21
1972	2,500	2	0.043	23
1973	1,200	2	0.011	7
1974	3,100	5	0.030	13
1975	21,400	22	0.052	17
1976	6,500	9	0.048	15
1977	14,700	31	0.017	10

*Estimated from the catch in trawls.
§Projected from mark-recapture estimates of population in April.

were scarce than in years when they were abundant (Forney, 1971). In the 1970's large year classes generally fared better than small ones, but the pattern was less consistent.

Reasons for differences in response of year classes to predation in 1961-1968 and 1969-1977 are evident when changes in predation and prey abundance during the two periods are examined (Table 15). A stable biomass of walleyes from 1961 to 1968 exerted constant predator pressure on perch year classes which varied in initial abundance. In contrast, walleye abundance fluctuated more widely from 1969 to 1977, and 3-fold differences in predator biomass would be expected to generate differences in mortality which would be independent of initial prey abundance. The depensatory effect of walleye predation on yellow perch cohorts was further obscured by fluctuations in the abundance of alternate prey. A successful year class of white perch increased the prey biomass in 1973 and probably contributed to low mortality of perch in a year when yellow perch density on August 1 was exceptionally low.

Success or failure of a perch cohort did not hinge solely on first-year survival as illustrated by the development of the 1970 and 1973 year classes (Table 13). Both year classes ranked as relatively weak in October at the end of the first growing season, but at age III these were clearly the dominant cohorts produced in the 1970's. Apparently mortality over winter or in the second year could drastically modify the contribution of a year class to the adult stock.

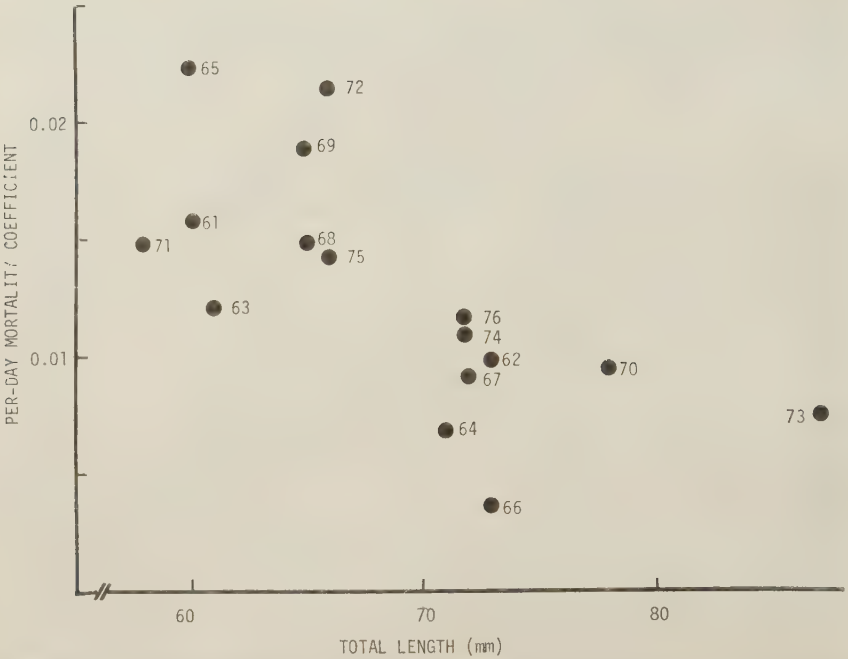

Figure 6. Per-day mortality coefficients for yellow perch between age 0 on October 15 and age I the following July-October in relation to their mean length at age 0 for the year classes from 1961 to 1976 (as represented by the numerals accompanying the plotted values).

A substantial proportion of the perch which disappeared between October of the first year and age III could be accounted for by examining the stomachs of walleyes (Nielsen, 1978). However, the rules governing the intensity of predation changed between age 0 and age I. Mortality was not depensatory as in the first year, but instead, the mean length of young perch at the end of the first growing season seemed to determine their subsequent survival (Figure 6). Cohorts which grew rapidly in their first year generally maintained their length advantage through age I which may have reduced their vulnerability to walleye predation. Early attainment of a large body size was clearly advantageous because few walleyes in Oneida Lake could ingest a perch over 16 centimeters long (Nielsen, 1978).

Year classes produced in the 1970's generally attained a greater mean length by September-October of their second growing season than earlier year classes (Table 16). The increased size of yearlings in later years of the study was probably a response to changes in the species composition of the zooplankton community (Figure 7). *Daphnia pulex* first appeared in large numbers in 1968 and by the 1970's had largely replaced *D. galeata* and *D. retrocurva*. Maturing at 1.7 millimeters, it was a more attractive prey than the other two which are smaller (1.0-1.2 millimeters). Occurrence of

TABLE 16. MEAN LENGTH OF YELLOW PERCH OF AGE 0 ON OCTOBER 15 AND OF AGES I AND II TAKEN IN TRAWLS DURING SEPTEMBER AND OCTOBER FOR THE YEAR CLASSES FROM 1960 TO 1976

Year class	Mean length (millimeters)		
	Age 0	Age I*	Age II*
1960	69	126 (67)	198 (38)
1961	60	136 (26)	174 (9)
1962	73	125 (92)	181 (27)
1963	61	137 (27)	191 (5)
1964	71	124 (197)	181 (45)
1965	60	125 (4)	165 (1)
1966	73	139 (81)	203 (107)
1967	72	138 (1,094)	198 (245)
1968	65	137 (379)	207 (10)
1969	65	146 (4)	216 (10)
1970	78	148 (661)	208 (149)
1971	58	125 (64)	199 (9)
1972	66	152 (5)	234 (11)
1973	87	153 (964)	222 (323)
1974	72	142 (137)	208 (43)
1975	66	142 (40)	218 (24)
1976	72	155 (87)	. .

*Figures in parentheses represent number of fish.

zooplankton in stomachs of age I and older perch increased substantially after 1969 (Clady and Hutchinson, 1976), and growth of age 0 perch was most rapid in years when *D. pulex* was abundant (Lin, 1975).

While walleye predation was the most probable explanation for the early demise of perch, the interplay of daphnid abundance and perch growth influenced the temporal distribution of mortality. In years when young perch were abundant (i.e., 1971, 1975 and 1977) *Daphnia pulex* populations collapsed in July. Their disappearance slowed the growth of perch which in turn increased the vulnerability of yearling perch to predation. Thus the 1971 and 1975 year classes, which were numerically abundant at age 0, suffered high mortality at age I and contributed fewer perch to the adult stock than year classes which were considerably smaller at age 0.

There was strong circumstantial evidence from the pattern of cohort development that walleye predation was responsible for most mortality of perch. But to predict the response of the perch population to a change in walleye abundance required more specific information. How many perch could a walleye eat and what was the shape of the relationship between walleye consumption and perch density? Was perch vulnerability to walleye predation a function of relative size, spatial distribution or abundance of alternate prey? These were the kinds of questions usually answered by observing predator and prey in the laboratory, but predator-prey interactions are difficult to duplicate in the confines of an aquarium. The alternative was to treat the lake as the experimental unit. The catch of perch in Miller samplers when cohorts averaged 18 millimeters provided an estimate of density at about the time walleyes began preying on young perch. The number of perch remaining in the fall could be approximated

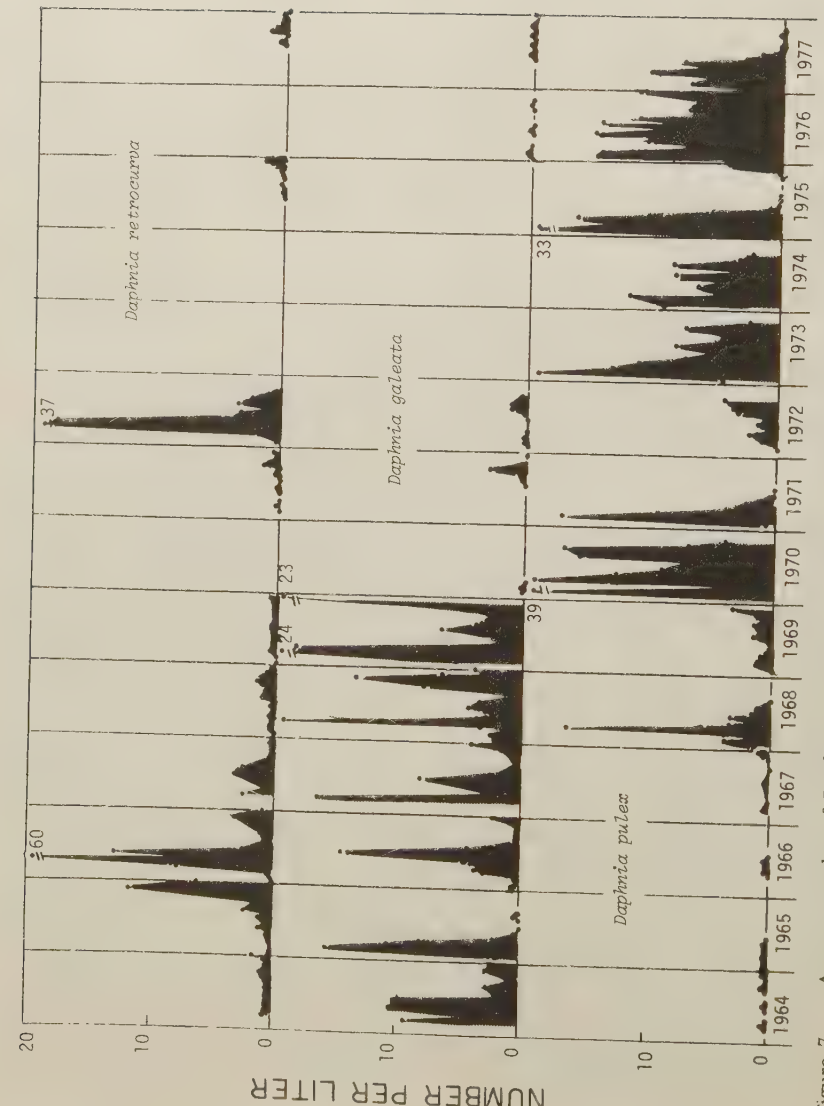

Figure 7. Average number of *Daphnia* per liter in plankton samples from Oneida Lake in May-October from 1964 to 1977.

from the catch and area swept by trawls, and periodic examination of walleye stomachs would provide estimates of the daily loss to predation. Thus the stage was set for a lake-size study of the predation process.

Daily consumption of age 0 perch by walleyes was estimated from the number of young observed in stomachs and the rate of gastric evacuation (Forney, 1977a). Examination of walleye stomachs collected at 4-hour intervals showed that perch were consumed at night and stomachs were evacuated during the day. The time required to evacuate the stomach was determined from the decrease in weight of prey in the stomachs of walleyes during the day. Small perch were evacuated more rapidly than large individuals, but during most of the summer the number of fish remains in the stomachs of walleyes collected at sunrise represented the daily meal. The number of perch consumed per day per kilogram of walleye weight declined from 100-200 in June when perch weighed less than 0.3 gram to fewer than 10 in late summer when perch averaged 2-7 grams. The numbers of perch consumed per kilogram were multiplied by the walleye biomass, and daily estimates were summed over the period of June to October.

Comparison of the numbers of perch consumed and the density of the perch population in June dispelled any doubts about the efficiency of the walleye as a predator (Table 17). Numbers of perch eaten by walleyes approached or exceeded estimates of the numbers of young perch available in June. Although predators cannot eat more prey than are available, estimates of prey density and consumption are subject to error and anomalous values would be expected if a high proportion of each perch cohort was consumed.

Older perch also preyed on young perch, but their share of the cohort was relatively small (Table 17). The incidence of perch cannibalism typically peaked in August (Tarby, 1974) and was most intense in years when the density of young was high as illustrated by the numbers consumed in 1971 and 1975. By the time cannibalism peaked, walleyes had already consumed two-thirds of the perch year class, which reduced the

TABLE 17. DENSITY OF AGE 0 YELLOW PERCH IN JUNE AS ESTIMATED FROM THE CATCH IN HIGH-SPEED SAMPLERS, AND THE NUMBER OF PERCH CONSUMED BY WALLEYES AND ADULT PERCH FROM JUNE TO OCTOBER, FOR THE YEARS 1971 TO 1977

Year	Period	Density of age 0 perch*	Number of perch consumed*	
			Walleye	Adult perch
1971	June 13 - October 2	216,000	242,900	56,210
1972	June 4 - September 30	121,000	80,730	4,200
1973	June 18 - October 28	17,000	17,940	590
1974	June 14 - October 26	32,000	29,400	330
1975	June 8 - October 19	189,000	204,530	23,900
1976	June 16 - October 16	47,000	35,800	100
1977	June 6 - October 18	65,000	70,000	9,080

*Per hectare.

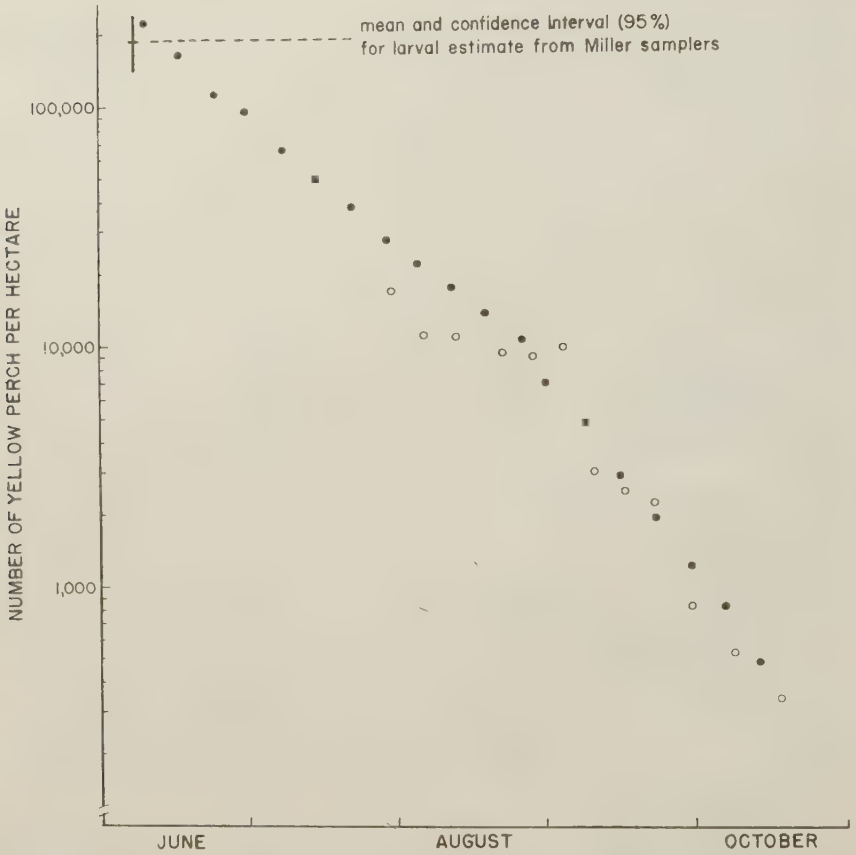

Figure 8. Density of age 0 yellow perch in 1975 as reconstructed from the number consumed by walleyes and older perch (solid circles). Density of larval perch in June from catch in Miller samplers and the number of perch taken per unit area swept by trawls in August-October (open circles) are independent estimates of abundance.

potential impact of cannibalism on the abundance of young perch (Forney, 1977a). In years when young perch were scarce, older perch switched to invertebrates (Tarby, 1974) while walleyes, which apparently had fewer energetically profitable options, continued to feed on young perch (Forney, 1974).

If most of the mortality of young perch was attributable to predation by walleyes and adult perch, as seemed likely, perch cohorts could be reconstructed by adding to the number remaining in October the number eaten in preceding weeks (Figure 8). The decrease in numbers of perch as portrayed by reconstructed populations for the period 1971 to 1977 suggested a fairly constant exponential rate of mortality from June to October. The same mortality pattern was evident in examining trawl catches

in late summer. The parallel decline was reassuring evidence that reconstructed populations were close antilogs of real populations.

Reconstruction of perch cohorts was more than a neat academic exercise. Estimates of perch density from reconstructed populations could be compared with numbers of perch in walleye stomachs to determine rates of predation and the factors controlling the intensity of predation. Models could then be constructed to examine the consequences of varying the walleye biomass.

The biomass of young perch from June to October was simulated with the biomass of walleyes in June set at 10 and 30 kilograms per hectare (Figure 9). Values for the initial density and growth of perch were those observed in 1971, and rates of walleye predation were derived from an analysis of data collected from 1971 to 1975 (Forney, 1976b). With a

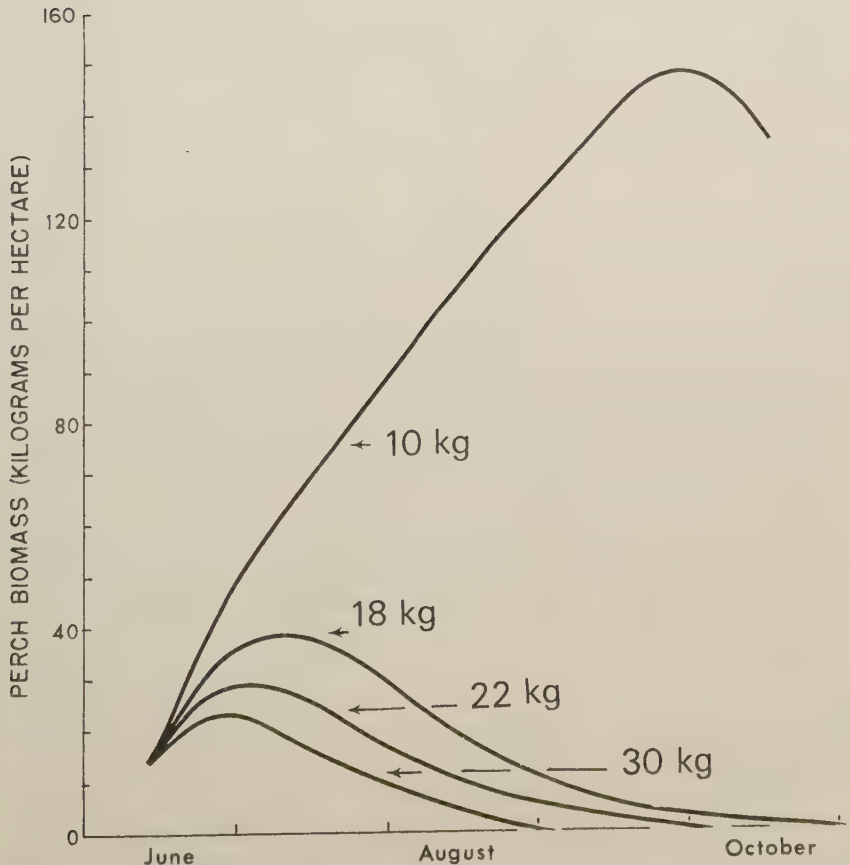

Figure 9. Simulation of the biomass of age 0 yellow perch from June to October with the biomass of walleyes in June set at 10 to 30 kilograms per hectare.

walleye biomass in June of between 18 and 30 kilograms per hectare, the biomass of young perch peaked in late June to early July and then declined in late summer as the weight of perch consumed exceeded production by the perch cohort. However, a further reduction in walleye biomass to 10 kilograms per hectare allowed the perch biomass to increase continuously through September. The sharp rise in perch biomass occurred as walleyes became satiated and rates of predation declined.

Although a high walleye biomass minimizes the risk that perch will swamp the predator population, as illustrated in Figure 9, a different management strategy is needed to optimize walleye production. Walleye production was roughly proportional to production by young perch from June to October during the period 1971 to 1977, except in 1973 when young white perch were abundant (Table 18). This suggests that the

Table 18. Production (grams per square meter) By Age III and Older Walleyes and Age 0 Yellow Perch From June to October During the Years 1971 to 1977

Year	Production		Trophic level efficiency
	Walleye*	Yellow perch*	
1971	1.334	12.98	0.103
1972	0.393	2.01	0.195
1973	0.561	1.78	0.315
1974	0.398	2.33	0.171
1975	1.170	9.49	0.123
1976	0.255	2.23	0.114
1977	1.113	9.74	0.114

*Sum of weekly estimates of production by the method of Chapman (1967).

highest walleye production will occur when the walleye biomas is held at a level which will optimize the yield from a cohort of young perch. The problem is somewhat analogous to predicting the level of fishing effort which will optimize the yield from a fishery. The number of perch harvested by walleyes must be low enough to allow the perch production to rise in early summer but large enough to consume most of the production in late summer.

Holding the walleye biomass at a low level to maximize walleye production conflicts with the equally desirable goal of maintaining a high walleye biomass to minimize the risk of prey swamping the predator population. Even if harvest regulations could be used to fine-tune walleye abundance (which they cannot), 10-fold fluctuations in the numbers of young perch could destabilize a delicate balance between perch production and walleye consumption. The modeling scenario seemed to suggest that any effort to increase walleye yield would reduce community stability. Johnson (1976) and Svardson and Molin (1973) had expressed similar concerns about the risks inherent in harvesting the dominant species in predator-prey associations. Whether the risks of destabilizing the community were real or imagined could not be easily tested, but it seemed likely that the level of

walleye biomass which would optimize yield was precariously close to the level which would trigger a dramatic increase in prey abundance.

The price of focusing on walleye-perch interactions was near ignorance of the role of other prey in the system. There was circumstantial evidence that walleye predation suppressed some species and restricted the distribution of others. Survival of white perch from the fingerling to adult stage was highest in years when young yellow perch were abundant, which suggested that young yellow perch served as a buffer reducing predation on white perch (Forney, 1974). Buffering induced synchronous fluctuation in the year-class strength of yellow perch and white perch, and similar synchrony in year-class abundance was evident in catches of other species (Clady and Nielsen, 1978). Inability of many species to invade open water may also be a tribute to the intensity of walleye predation. In Oneida Lake, spottail shiners and emerald shiners were rarely taken in trawls, but in Lake Erie, where the walleye has declined, these shiners are often the predominant species in trawl catches.

While the effect of secondary prey on walleye-perch interactions was difficult to pinpoint, there was reason to suspect that some of the variability

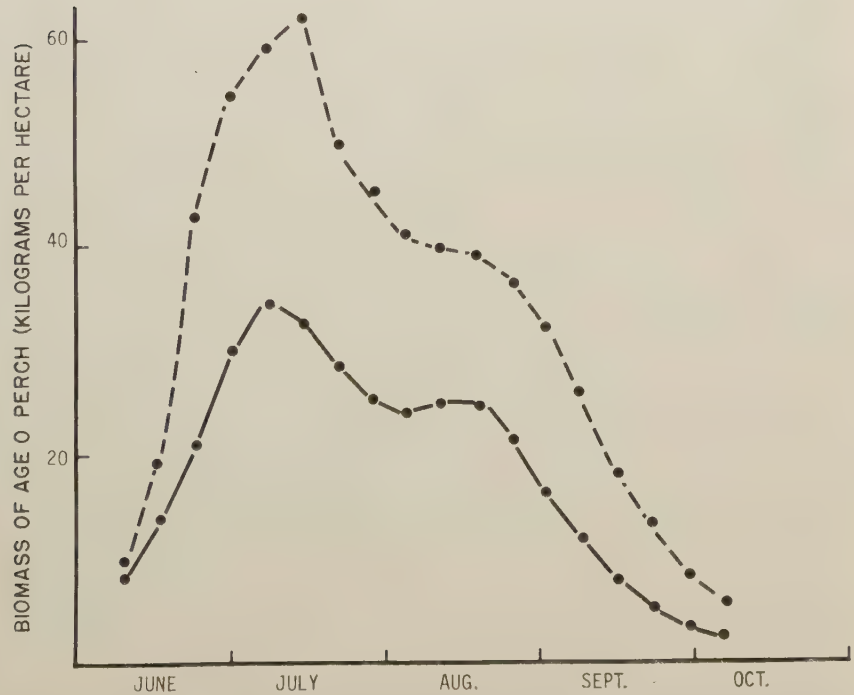

Figure 10. Biomass of the 1975 cohort of age 0 yellow perch as reconstructed from the numbers of perch recovered from stomachs of walleyes and adult yellow perch (solid line) and biomass of the cohort based on assuming a 2-week delay in the time predation began (dash line).

in survival of perch during the pelagic stage was attributable to fluctuations in the abundance of alternate prey. Examination of reconstructed perch cohorts suggested that a two-week delay in the time walleyes began preying on perch in June could double the production and biomass attained by a cohort during the summer (Figure 10). In the early years of this study the mayfly, *Hexagenia limbata*, was important in the diet of walleyes from mid-June to mid-July, while in later years chrionomids and young ciscoes replaced it as the alternate prey. Although early survival of perch could not be directly linked to the abundance of these alternate prey, the decline and eventual extinction of the mayfly in the 1960's (Jacobsen, 1966; Clady and Hutchinson, 1976) was followed in the 1970's by a period of low fingerling density and biomass among perch (Table 15). One can only speculate that the mayfly was a more attractive alternate food and perhaps prolonged the survival of young perch, enabling year classes to attain a higher biomass.

Seven years of peering into the stomachs of walleyes and perch had answered some questions and raised more. Most young perch were the victims of predation by walleyes, and those not eaten by walleyes were consumed by their progenitors and an array of less numerous predators. Reducing the abundance of walleyes would increase perch survival, but how much was uncertain. Year classes of perch which were most abundant as young often fared poorly as yearlings. This within-cohort compensatory mortality was probably a consequence of density-dependent growth mediated by changes in zooplankton composition. It was clear that reducing walleye biomass would increase the survival of young perch and lead to more and probably smaller yearling perch. Presumably walleye predation on yearling perch would increase, but the effect of changes in the age and size structure of the perch population on walleye recruitment and the abundance of subordinate species could not be predicted.

The message for managers was one of caution. There were signs that walleye production and yield could be increased, at least temporarily, by more intense harvest. Removal of walleyes would enable more young perch to reach a larger size before they were consumed, and food was the factor limiting walleye production. The trick is to retain a large enough biomass of walleyes to cope with variations in prey abundance. Should a period of low walleye biomass coincide with an exceptionally successful hatch of perch, the predators would be swamped. Rapid expansion of prey might cause shifts in species abundance which would be difficult to reverse. Thus, the manager has the unenviable task of balancing the value of an increase in harvest against a risk which research has yet to assess.

EIPLOGUE

The species composition and size structure of the Oneida Lake fish community are largely a fortuitous outcome of man's activities. Canalization,

destruction of wetlands and probably less easily identified cultural changes in the early 1900's nearly eliminated the eel and esocids, while the walleye flourished. Records of the Oneida hatchery indicate that the catch of walleyes in trapnets rose between 1930 and 1940 at about the time esocids were declining (Forney, 1977b). Evidence that the contemporary walleye population is food-limited suggests that the increase in walleyes was a response to reduced interspecific competition.

Although esocids and eels occupied the littoral area, their loss had little detectable effect on the species composition of the inshore fish community. Yellow perch was the species taken most frequently in shore seining from 1915 to 1927 and it was clearly the predominant species from 1960 to 1970 (Clady, 1976b). However, perch were smaller and their growth was less rapid in the earlier years. Most perch caught in the 1920's and 1930's were less than 20 centimeters long (W. A. Dence, personal communication), but by the 1950's the majority of yellow perch in the angling catch and experimental gear were 23 to 30 centimeters long with few under 20 centimeters. The increase in growth of perch was probably a response to changes in the distribution of mortality during early life. Expansion of the walleye population would be expected to intensify predation on smaller, younger perch, which would reduce yearling density and favor more rapid growth at age I and II.

Had the elimination of eels and esocids been planned, the transition to a walleye-perch association could be cited as a phenomenal management success. The walleye is the preferred sport fish, and the increase in size of perch was an added bonus. The transition from a diverse predator population to one dominated by the walleye did not seriously disrupt the community. Although some cyprinids declined, centrarchids showed little change in abundance and yellow perch retained a position of dominance. The new equilibrium between walleyes and yellow perch has persisted for several decades, but a change in physical conditions, the invasion of a new species or either insufficient or excessive harvesting could abruptly alter the community.

The equilibrium between walleyes and perch is maintained by the interplay between prey abundance and walleye cannibalism. High prey production reduces cannibalism and increases walleye recruitment, but the increase in walleye biomass must eventually suppress prey abundance and increase cannibalism. Density-independent fluctuations in prey abundance and time lags which generate an imbalance between predator biomass and prey production prevent the development of a stable equilibrium. The invasion of Oneida Lake by white perch followed by a brief but explosive increase in gizzard shad probably precipitated the erratic fluctuations in walleye recruitment and stock biomass that characterized the 1950's. Although walleye recruitment stabilized in the 1960's, fluctuations reappeared in the 1970's after several years in which survival of young perch was low.

Destabilizing effects of changes in prey abundance on walleye abundance were amplified by angling exploitation. Walleyes were most vulnerable to angling in years when prey were scarce. Thus the harvest of adult walleyes was often high in periods which were least favorable for recruitment of strong walleye year classes. The combined effects of intense exploitation and low recruitment can drive the walleye biomass to low levels as illustrated by events in the 1970's. Should conditions enable prey species to flood the environment with young at a time when the biomass of walleyes was low, an abrupt expansion of subordinate species could threaten walleye dominance.

The problem facing the manager is how to balance the value of the annual walleye harvest against the risk of losing it through a sudden switch in species abundance. While a low walleye biomass can endanger community stability, maintenance of an excessively high walleye biomass will reduce walleye production and yield. To achieve the dual objectives of minimizing risk and optimizing yield, regulations must encourage the harvest of surplus stock when the biomass is high and restrict the harvest when recruitment and biomass are low.

The concept of tightening and relaxing regulations to optimize walleye yield was implemented by the Department as a management strategy in 1978. The minimum "safe" walleye biomass was set at 13 kilograms per hectare. The biomass of adult stock was approximated from the catch in trapnets set by the Oneida hatchery (Forney, 1977b), and the future contribution of younger age groups to the adult stock was predicted from the catch in trawls (Forney, 1978). The following criteria were established as a basis for setting angling regulations.

Population status	Recommended minimum length
Adult stock in April over 13 kilograms per hectare (15 pounds per acre) and sub-adult year classes (ages I, II and III) expected to contribute over 500,000 to adult stock	12 inches
Adult stock in April under 13 kilograms per hectare and sub-adult year classes expected to contribute 200,000 to 500,000 to adult stock	15 inches
Adult stock in April under 13 kilograms per hectare and sub-adult year classes expected to contribute 200,000 to adult stock	18 inches

Length limits are probably the most effective means of regulating the catch and are less likely to disrupt the fishery than restrictions on gear or length of season.

These few guidelines may seem a rather marginal return on a 20-year investment in research. But those who expect large gains in yield by fine-tuning sport fisheries will probably be disappointed. Early hopes of dramatically increasing the yield of walleyes were squelched by the discovery that exploitation was difficult to control through regulations, that the level of walleye biomass for high production was close to the threshold of community instability and that there were few "surplus" prey to support a larger predator population. In contemplating these frustrations, there was some consolation in the knowledge that, in other waters, years of perturbing, observing and theorizing about fish have seldom produced a more comprehensive set of management rules.

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SIMULATION OF THE INTERACTION OF DEER WITH NORTHERN FOREST VEGETATION[1]

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ABSTRACT

A computer simulation model of the interaction of white-tailed deer with northern forest vegetation is described. In a verification analysis, a simulated old-growth northern hardwood stand was shown to support a deer population density of less than one per square mile which conforms to values reported in the literature. In a sensitivity analysis, variations in the caloric density of forage of as little as 0.2 kilocalorie per gram were shown to cause tenfold differences in population density. In a simulated experiment it was shown that densities as high as five deer per square mile can be produced in partially cut hardwoods and that this density of deer can prevent regeneration of certain tree species.

Improved knowledge of forest ecosystems is required by both wildlife and timber managers. In the Northeast a better understanding of the interaction between white-tailed deer (*Odocoileus virginianus*) and forest vegetation is desirable. A model for predicting forest vegetation dynamics and deer browse production was described by Cooperrider and Behrend (1979). The present paper shows how this model can be linked to a deer population model to obtain an integrated model of the dynamics of both forest vegetation and deer populations. The paper describes the integrated model and how it can be used, gives examples of several simulation runs and discusses the strengths and weaknesses of the model. The data used represent observations at the Huntington Wildlife Forest near Newcomb in northern New York.

THE SIMULATION MODEL

The model consists of a set of algebraic instructions for manipulating data in order to mimic certain aspects of the dynamics of forest vegetation. It is implemented as a computer program written in FORTRAN IV for a CDC computer. Dynamics of the system are modeled by using a set of recurrence or difference equations, and as such it has been termed a finite difference model by Lassiter and Hayne (1971).

The model simulates four basic processes of such a deer-forest system, i.e., weather generation, vegetation dynamics, deer population dynamics,

[1]A contribution of the State University of New York College of Environmental Science and Forestry at Syracuse University. The authors wish to thank W. C. Tierson and T. Cunia for their advice and assistance during all phases of the project.

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and management of deer and vegetation. The submodel of vegetation dynamics was described in detail by Cooperrider and Behrend (1980) and is only mentioned briefly here.

NOMENCLATURE

For the purpose of the following discussion, a uniform nomenclature has been adopted which is consistent with that described by Bledsoe et al. (1971). The variables of the model can be considered to be of six types: principal system variables, intermediate system variables, driving variables, independent variables, system parameters and dummy function arguments. A hybrid system of metric and English units of measure has been employed in order to use data already collected according to one system or the other.

INITIAL INPUTS

Two types of variables must be supplied at the beginning of a computer run: principal system variables and system parameters. The principal system variables pertain to the forest vegetation and the deer population. Forest vegetation is represented in the model by from 1 to 15 different types or strata. Each stratum is characterized by the vegetation on it and its total acreage, thus comprising all areas within the forest that have such a vegetation structure. Strata are used only to quantify this structure on areas that have similar vegetation; they imply nothing about the spatial pattern of such areas. The variables describing the forest vegetation consist of the number of stems per acre by size class for each tree or shrub species. The variables describing the deer population consist of the total number of deer plus three attributes of individual deer: sex, age and live weight.

System parameters govern the interaction of the variables. Those required for simulating the biological processes of the system were listed in detail by Cooperrider (1973) and are noted in the following description of the model dynamics for each process.

WEATHER GENERATION

Weather generation is derived from a set of subprograms for (1) choosing one or more years of actual weather records (maximum temperature, minimum temperature and snow depth) at a base station[3] and (2) calculating from them a predicted weather pattern for each stratum in the forest. Within a stratum, each weather factor is treated as a function of the

[3]The weather data used in this study consisted of 20 years of records (July 1951 through June 1971) of maximum daily temperature, minimum daily temperature and snow depth from the weather station (Newcomb 4NW) of the U.S. National Oceanic and Atmospheric Administration on the Huntington Wildlife Forest.

base station values and the basal area of conifers per acre[4] within that stratum. Using the predicted values for temperature and snow depth, together with the basal area of conifers, the level of deer-supporting crusts under different postulated conditions is predicted for each stratum, and this information is used to estimate how much of the total browse present is available to deer during the winter.

The equations and values used for predicting weather patterns were derived, graphically and by least squares curve fitting, from data reported by Hepburn (1959) and Ozoga (1968). The rationale for using the basal area of conifers per acre to predict weather variables is that an overstory of conifers insulates the microclimate in the understory and, as its density increases, results generally in lower maximum daily temperatures, higher minimum daily temperatures and lower snow depths during the winter. Basal area of conifers is correlated with canopy closure of conifers and thus provides a useful concomitant variable for prediction. However, the modification of temperature due to the conifer canopy is rather slight. In any case, the temperature values derived are used only to predict formation of supporting crusts; they are not used to predict deer behavior.

Vegetation Dynamics

The procedure for modeling vegetation dynamics was described in detail by Cooperrider and Behrend (1980). In general, growth and mortality of stems and weight of browse per stem are predicted as a function of stand density as measured by basal area per acre. However, two modifications of the vegetation dynamics submodel must be made in order to account for the effect of deer browsing on the vegetation.

In this submodel, stems are divided into discrete height and diameter (i.e., diameter breast height) classes for each species. At yearly intervals, the expected numbers of saplings moving from one height class to a higher class are calculated as a function of transition rates. To account for the effect of deer browsing, transition rates are applied only to those stems whose terminal has not been browsed, i.e., only unbrowsed stems are moved from one size class to a higher one. Thus, deer browsing is modeled as affecting growth of stems but not their vigor or mortality.

A second modification is the inclusion of a measure of available herbaceous material. This variable is a function of time only and is intended to represent all edible green herbaceous material that is available to deer, including all current growth of grass and forbs as well as the non-woody growth of trees and shrubs. For most simulations, this parameter was specified as 1 kilogram per acre for the period June 1 to October 1 and as zero otherwise.

[4]The basal area of conifers per acre represents the sum of the basal areas of all individual coniferous trees over 1 inch in diameter. The basal area of an individual tree is defined as $\pi D^2/4 \times 144$, where D is diameter at breast height in inches.

DEER POPULATION DYNAMICS

This process can be divided into three categories: feeding, birth and death.

FEEDING The feeding routines are repeated for each deer on a weekly basis. Deer feeding is modeled as consisting of three phases, i.e., choice of forage, forage removal and change in body weight of deer (growth).

Choice of forage is modeled as an activity by which a deer continuously maximizes its digestible energy intake subject to constraints as to the amount of available forage, the digestible energy content and the capacity of the animal itself. The following procedure is carried out for each deer for the appropriate time interval.

First, the weight of available browse in each stratum is calculated as a function of the amount present, the depth of snow, the level of a deer-supporting crust and the height to which a deer can reach. An additional restriction is placed on food availability to account for the limitation on how much ground a deer can or will cover in foraging in a day.

Then, the digestive capacity (maximum daily forage intake) of deer is derived according to the equations shown in Table 1. For young animals, capacity is calculated as a function of weight. For adults, a maximum capacity is calculated as a function of season by specifying a mean capacity and a sine wave fluctuation around this mean. For females the peak intake comes on October 1, reflecting the observed trend that food consumption is lowest in mid-winter and then gradually increases with pregnancy and lactation after which it drops off again in late fall (Ozoga and Verme, 1970). For males the peak intake comes on June 1, reflecting a low intake by adult bucks during the rut followed by a gradual increase until summer (Severinghaus and Cheatum, 1956). In the model, the value for immature deer is used unless it exceeds that for adults in which case the latter is used.

Next, the total digestible energy intake the deer can obtain from each stratum is calculated by an algorithm that maximizes the digestible energy

TABLE 1. EQUATIONS FOR CALCULATING THE DIGESTIVE CAPACITY OF DEER

Age and sex	Equation*
Immature§	
Male	$C = 42 \times Wt^{0.97}$
Female	$C = 69 \times Wt^{0.80}$
Adult†	
Male	$C = 2400 + 600 \times \text{Sin}(6.28 \times XWK/52)$
Female	$C = 2000 + 500 \times \text{Sin}(6.28 \times XWK/52)$

*In which: C = digestive capacity (maximum daily forage intake) in grams of dry weight per day.

Wt = live weight in kilograms.

XWK = number of weeks after February 1 for males, after July 1 for females.

§After Norden et al. (1970) and represent data for young black-tailed deer.

†Derived graphically from data for white-tailed deer given by Long et al. (1965).

intake by simply choosing species with the highest digestible energy density until either the capacity of the deer is reached or the browse supply is exhausted. The stratum chosen is then the one with the highest total available digestible energy.

To determine the total digestible energy, the caloric density (kilocalories of digestible energy per gram of oven-dry weight) is calculated for each species. This is done by specifying a mean and an amplitude of variation for each species and computing the caloric density as

$$Y = (MN - AMP) + (R \times 2AMP)$$

where

Y = predicted caloric density
MN = mean caloric density for the species
AMP = amplitude of variation
R = a random number ($0 > R > 1.0$)

The parameter values used for most simulations are shown in Table 2.

The subprograms for forage removal merely subtract the forage eaten by the deer from the forage available for each species by a random procedure.

Table 2. Parameters For Caloric Density of Deer Forage As Used in Simulation Model

Species	Caloric density*	Source§
Hardwoods		
Sugar maple	2.5	Estimate
Yellow birch	2.4	Estimate
White ash	2.0	Estimate
Red maple	1.5	†
Beech	1.4	Estimate
Miscellaneous	2.0	Estimate
Conifers		
Hemlock	2.5	†
Red spruce	0.0	Estimate
Miscellaneous	2.0	Estimate
Shrubs		
Witchhobble	2.4	†
Striped maple	1.7	†
Miscellaneous	2.0	Estimate
Herbaceous forage		
Miscellaneous	3.0	‡

*In kilocalories of digestible energy per gram of dry weight. Values are means, all with a range of ± 0.2.

§Estimates based on species of known caloric density that are similar in palatability and preference.

†Mautz and Silver (1972) reported values as follows: red maple-1.3; hemlock-2.4; witchhobble-2.6; striped maple-1.5.

‡Whelan et al. (1972) reported values ranging from 2.2 to 3.3 for mixed diets of forbs.

Change in body weight of deer is calculated as a function of body weight and digestible energy intake by using the equation

$$Y = B_1 + B_2 (X/W^{0.75})$$

where

Y = growth in kilograms
X = digestible energy intake as kilograms
W = body weight in kilograms
B_1 and B_2 = fitting parameters

The parameters used for all simulations were $B_1 = -0.1933$ and $B_2 = +0.001210$ as reported by Ullrey et al. (1969) for white-tailed deer.

In summary, deer feeding is modeled as a transfer process which is controlled by an optimization routine wherein the efficiency of the transfer or conversion of plant biomass of a given caloric density to an animal biomass is governed by the foregoing equation. The major feedback effect on vegetation dynamics is the effect of deer browsing on the growth of saplings.

BIRTH Birth and associated factors in the model are of two types: addition of new members into the population according to specified birth rates, and modification of weights and feeding routines among females to account for lactation and weight loss at the birth of fawns. Details of these procedures were described by Cooperrider (1973).

DEATH Mortality may be divided into that caused directly by starvation and that caused by other factors (predation, disease and accidents). Mortality due to hunting is discussed separately under management.

Death by starvation is treated as a function of body weight with a critical weight being specified for each sex and age group. Each time a deer's weight changes, it is compared with the critical weight; if it is less than the critical weight, the deer is considered to have died of starvation and is removed from the population. Generally, a deer is considered to have died of starvation when it has declined to 70 per cent of a normal fall weight, as Davenport (1939) reported a 30 per cent weight loss to be near the maximum for growing animals.

Non-starvation losses are calculated once a year, normally at the end of March, as a function of a set of annual mortality rates. As with birth rates, these may be fixed (proportional mortality) or they may be a function of density (density-dependent mortality), and they may be the same or different for various sex and age groups.

MANAGEMENT OF DEER AND VEGETATION

Management options simulated by the model are of two types: deer harvest management and forest vegetation management. Removal of deer from the population by hunting may be imposed on the system in a

number of ways by specifying mortality rates. These rates may be fixed or density-dependent. A quota harvest may also be employed to remove a fixed number of animals. As with the other forms of mortality, the quotas may be specific for each sex or age group. The only type of forest vegetation management that the model allows is removal of trees over 1 inch in diameter. This is done by specifying either a number or a percentage of trees to be removed. The harvest may be specified for all species and strata, or separately for each species, stratum or diameter class.

SIMULATION EXAMPLES

Simulation procedure can be conveniently divided into three categories: verification analysis, sensitivity analysis and computer experimentation. An example of each is presented.

Verification Analysis

Verification of a model generally involves comparing results of simulation runs with known data in order to test the model in a situation where the real-life conditions are fairly well understood or documented. Verification analyses are therefore a measure of how accurately a model mimics

Table 3. Basal Area Per Acre For Various Tree Species in Actual and Simulated Stands of Old-growth and Cutover Northern Hardwoods* on the Huntington Wildlife Forest

Species	Basal areas§			
	Old growth		Cutover	
	Actual†	Simulated	Actual‡	Simulated
Hardwoods				
Sugar maple	91	90	26	25
Beech	50	50	8	7
Yellow birch	13	14	20	20
White ash	0	1	0	1
Red maple	0	0	0	1
Miscellaneous	0	0	0	1
Sub-total	154	155	54	55
Conifers				
Red spruce	3	5	1	1
Hemlock	0	0	3	3
Miscellaneous	0	0	0	1
Sub-total	3	5	4	5
Total	157	160	58	60

*As a forest type "northern hardwoods" includes some conifers.

§In square feet per acre.

†An uncut stand; data derived by point sampling.

‡Stand cut in 1968 and 1969; data derived by plot sampling shortly after cutting was concluded.

Figure 1. Simulated deer population density in old-growth northern hardwoods over a 30-year period.

the real-life situation and can thus be used to gauge how much credence should be given to model predictions in situations where the process is not well understood.

The deer population density in old-growth forests may be used as an example. Although deer biologists disagree on many issues, there is some agreement that uncut old-growth timber supports a relatively low density of deer. Furthermore, this density is in general the minimum that can be supported by a piece of undeveloped land. As such, it is a good situation to simulate for the purpose of verification since one can predict from biological knowledge that the density there will be very low and that densities on cutover areas should be as high or higher.

A preliminary simulation indicated that, with an initial density of 0.5 deer per square mile and the usual restrictions on availability of browse, no deer could survive a full year in a pure old-growth stand. Even with an initial density of 0.1 per square mile, a deer population could not be sustained. However, when the constraint on browse availability was relaxed, deer densities in the order of one per square mile could be maintained.

Simulated and actual basal areas per acre for various tree species in old-growth stands are shown in Table 3, and the simulated deer population density for a 30-year period is shown in Figure 1. These results suggest that densities in the order of one deer per square mile could be supported in old-growth northern hardwoods if a deer could cover as much ground per day as necessary to optimize its browse intake. This implies, however, that the actual density that can be supported is less and emphasizes the sensitivity of the model to the parameter which specifies how much area a deer can browse over in one day.

The population shows a pattern of exponential growth followed by a crash such as is known to occur in ungulate populations as discussed by Caughley (1970). The crash is due primarily to starvation of fawns and yearlings as well as adult females. Whitlock and Eberhardt (1956), reporting on a large-scale survey of dead deer in Michigan, found that all deer that died of starvation were either young animals or old females. It is interesting that this reduction in the percentage of females in the population tends to confer stability by reducing the over-all productivity.

Unfortunately, precise quantitative knowledge of population densities in mature hardwood forests is not available. Dasmann (1971) stated that mature coniferous forests on the West Coast often support fewer than two deer per square mile. The simulation experiment described here suggests that sustainable deer densities in mature northern hardwood forests are even lower; nevertheless, field verification of this conclusion would be desirable. In general, however, the phenomenon of low deer density in mature hardwood forests was realistically mimicked by the simulation

Table 4. Parameters Used For Sensitivity Analysis of Caloric Density For Various Tree Species

Species	Deviation from mean caloric density*				
	−0.2	−0.1	0.0	+0.1	+0.2
Hardwoods					
Sugar maple	2.3	2.4	2.5	2.6	2.7
Beech	1.2	1.4	1.4	1.5	1.6
Yellow birch	2.2	2.3	2.4	2.5	2.6
White ash	1.8	1.9	2.0	2.1	2.2
Red maple	1.3	1.4	1.5	1.6	1.7
Miscellaneous	1.8	1.9	2.0	2.1	2.2
Conifers					
Red spruce	1.5	1.6	1.7	1.8	1.9
Shrubs					
Witchhobble	2.2	2.3	2.4	2.5	2.6
Miscellaneous	1.8	1.9	2.0	2.1	2.2
Herbaceous forage					
Miscellaneous	2.8	2.9	3.0	3.1	3.2

*In kilocalories of digestible energy per gram of dry weight. For all values the range was ± 0.2.

model. Higher densities in cutover forests are confirmed by the following examples.

SENSITIVITY ANALYSIS

A second category of simulation procedure is sensitivity analysis which is designed to determine how "sensitive" the model is to certain interrelationships, i.e., how much a change in a given parameter will affect a principal system variable. Sensitivity analysis can also provide insight into the relative importance of components of a model in affecting the behavior of the system. One such analysis tested how the size of a deer population (a principal system variable) was affected by small changes in the caloric density of its food (a parameter). The actual parameters used are shown in

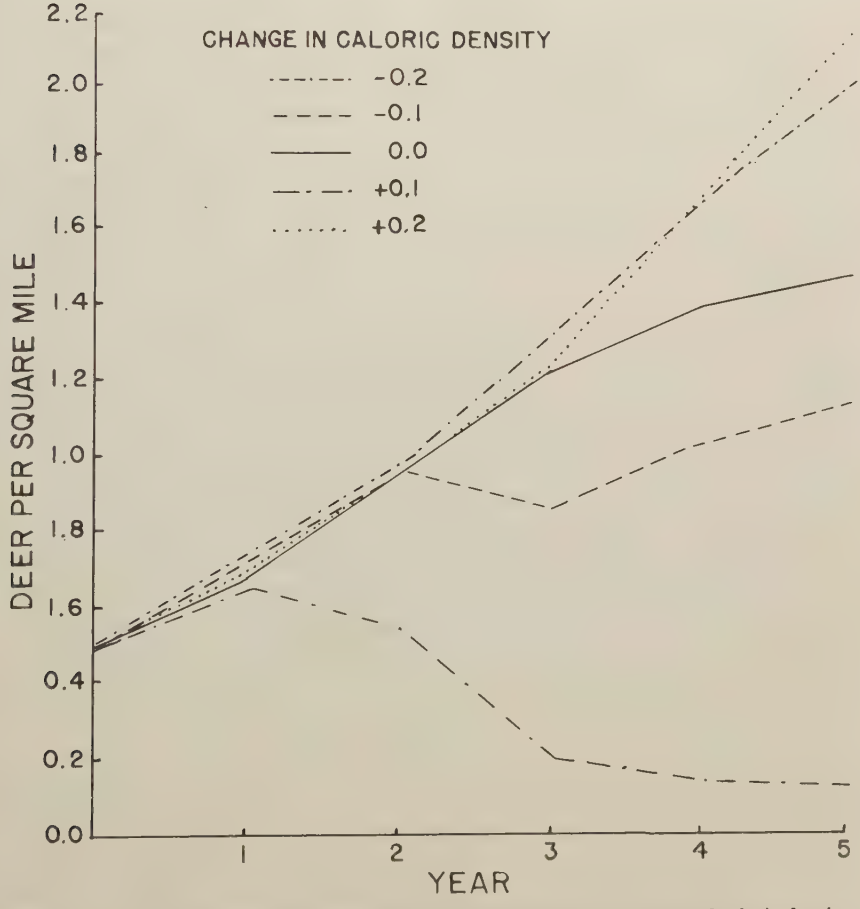

Figure 2. Trend in density of a simulated deer population at five levels of caloric density in their food over a 5-year period.

Table 4, and the response of a simulated deer population, in terms of density, to the average values for five levels of caloric density in the food consumed over a 5-year period is shown in Figure 2. Differences in the estimated mean caloric density of 0.4 kilocalorie of digestible energy per gram were shown to produce tenfold differences in population density.

The implications for research and management are clear. If one accepts the logic of the model, there is a strong indication that the caloric density of browse is a prime factor governing deer population density. Since many of the caloric density parameters used represent little more than educated guesses, these results suggest a need for more effort to obtain good estimates of these values for the common browse species. Furthermore, the effect of interaction on the digestibility of browse in mixed rations needs to be determined.

Computer Experimentation

Computer experiments allow the user to test hypotheses about the deer-forest system by simulating various situations with the model. Such experimentation provides insight into the processes associated with the system. Clearly, any conclusions drawn from computer experiments should be regarded as only tentative and subject to empirical verification. However, because the computer can simulate in a few minutes a situation that would take years to develop in nature, the knowledge gained is potentially valuable in both directing future research and making management decisions.

The effect of timber cutting on deer population density is an important management consideration. An experiment was run using the data for old-growth and cutover stands given in Table 3. The simulated deer density for 20 years following cutting is shown in Figure 3. As one would expect, the predicted density supported for the first few years in the cutover area is far higher than that in the old-growth area. However, with no hunting, the population soon overshoots a density that can be supported and crashes. The overshoot and crash occur even though browse production declined steadily throughout the period (Cooperrider, 1973).

Such results help to clarify the relationship between deer population density and browse availability in the forest. Simulation of the vegetation in the cutover area also revealed that very few stems are growing out of reach of deer and that the increase in basal area over the period is primarily due to growth of residual trees. In short, a simulated year-around population of about three deer per square mile can prohibit regeneration under the given conditions.

DISCUSSION

The assumption that deer browsing directly affects growth but not mor-

Figure 3. Simulated deer population density in cutover northern hardwoods over a 20-year period following cutting

tality of the forage plants is a critical one. There is little evidence for most of the species considered that browsing of current growth increases mortality. Jordan (undated) reported that simulated browsing on sugar maple, red maple and white ash produced only negligible mortality. Wiersma (1968) also found no mortality on clipped stems of sugar maple. Gould (1966) reported no mortality on clipped witchhobble plants, but he did suggest that continued heavy browsing can cause mortality of individual plants and cited evidence that deer have caused the near extirpation of this species in some areas. In general, the species modeled in the present study are fairly tolerant of deer browsing, but other species may not be as tolerant and if their dynamics are to be simulated the model should be modified accordingly.

One of the greatest limitations of the model is that spatial distributions are not considered. Although a number of separate strata can be simulated, they are essentially treated as if they all exist in one point in space. Therefore, the energy cost to a deer of moving from one stratum to

another is assumed to be negligible. Depending on the spatial pattern of the vegetation and the time of year, this may be a very unreasonable assumption. Sensitivity analyses and other experiments have shown that the "availability" parameter, i.e., the number of acres a deer can forage over per day, is quite critical in determining a sustainable population density. This suggests that the energy cost of obtaining food is an important aspect of deer ecology and that efforts are needed to investigate and quantify this phenomenon and to relate energy cost to spatial patterns of vegetation. As Pielou (1969) pointed out, few ecological models have integrated consideration of spacial patterns with time patterns (population dynamics) or organisms. Generally the two subjects are treated separately. Those designing future models of deer population dynamics should strive to realistically incorporate spacial considerations and constraints.

Naylor et al. (1966) noted that verification of simulation models remains one of the most difficult of the unresolved problems of computer simulation techniques. A number of statistical techniques can, of course, be applied to compare results of simulation runs with historical data. However, the interpretation of such statistics is more difficult, and there are a number of unresolved philosophical problems associated with verification. A specific problem with verification of deer population models is the scarcity of good population density estimates. Without such estimates it is difficult to compare and verify model predictions.

The usefulness and accuracy of computer experiments are dependent on both the realism of the model and the precision of the parameters. It is the authors' belief that any conclusions drawn from modeling should be regarded as tentative and subject to empirical verification. Levins (1966) suggested that a principal value of a good model is that it can generate good testable hypotheses. The usefulness of the model described here depends on how well it can suggest explanations for observed phenomena and help to focus research efforts on critical areas that need clarifying.

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THE AMERICAN LOBSTER AND THE POT FISHERY IN THE INSHORE WATERS OFF THE SOUTH SHORE OF LONG ISLAND, NEW YORK[1]

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ABSTRACT

Among American lobsters from the inshore waters off the south shore of Long Island, the first males to reach maturity were 46 to 50 millimeters in carapace length, and most were mature by the time they reached 56 to 60 millimeters. The first females to reach maturity were about 81 millimeters in carapace length, about half were mature at 90 millimeters and all longer than 100 millimeters were mature. In the total catch, males ranged from 36 to 165 millimeters in carapace length and averaged 83 millimeters, while females ranged from 19 to 155 millimeters and averaged 84 millimeters. Landed males averaged 98 millimeters in carapace length, and females 103 millimeters. Cull rates were generally less than 10 per cent for legal-sized lobsters and greater for sub-legal ones. A hurricane in August 1976 apparently increased the frequency of culls for several months following. The sex ration was essentially one to one. A length-weight relationship of $\log W = -3.2736 + 3.0989 \log L$ was derived. The incidence of a parasite indicative of lobsters having spent time in offshore waters was greater than that of one indicative of time spent in inshore waters. Lobsters from the study area appear to be of the same stock as those found in adjacent offshore waters, but to differ from those in Long Island Sound with respect to the size at which they reach maturity. For protection of females until at least about half become mature, a minimum size limit of 3½ inches (89 millimeters) in carapace length would be more desirable (biologically) than the present limit of 3 3/16 inches (81 millimeters). The great importance of the black sea bass and the Jonah crab to the fishery is discussed.

Most recent studies of the American lobster (*Homarus americanus*) in the vicinity of Long Island (N.Y.) have dealt with the resource in Long Island Sound (Briggs, 1976; Briggs and Mushacke, 1979; Lund and Stewart, 1970; Lund et al., 1973; Smith, 1977; Valenti and Peters, 1977; Weiss, 1975) or with the resource on the continental shelf and offshore canyons (Cooper and Uzmann, 1977; Skud and Perkins, 1969; Uzmann et al., 1977). Only Lund and Stewart (1970) and Briggs and Zawacki (1974) dealt with the resource in the inshore waters off the south shore of Long Island. The former were concerned with larval distribution; the latter, with aspects of the lobster population on two artificial reefs.

In this paper are presented the results of a 2-year (1976 and 1977) study designed to determine the size at maturity and sex ratio of lobsters from these south shore waters, as well as the size composition of lobster catches

[1]Contribution No. 80-1 of the Division of Marine Resources. This research was funded in part through the Commercial Fisheries Research and Development Act (Public Law 88-309) under Project 3-257-R. The authors wish to thank the cooperating fishermen (who desire to remain anonymous) for permitting the collection of data aboard their boats, and also John C. Poole, Chester S. Zawacki, Samuel L. Finkelstein, Thomas Elefterion, Egbert Howell, Albert Kilthau and Pieter Van Volkenburgh of the Division of Marine Resources who assisted in collecting the data.

Figure 1. Map of Long Island showing study area (cross hatched) in the inshore waters off the south shore.

and landings by commercial fishermen. Information was also gathered on length-weight relationships, the incidence of parasites indicative of lobsters having spent time in inshore or offshore waters and the importance of other marine animals (fish and crabs) in the catch and landings. The study could not have been accomplished without the cooperation of commercial fishermen who fished in the study area (Figure 1). Water depths where fishing was done ranged from about 10 meters to 30 meters, and distance from shore ranged from less than one to about 10 kilometers.

METHODS

The authors and/or assisting Department personnel accompanied cooperating commercial fishermen on 13 trips in the study area, and the data recorded were augmented by data obtained on 15 trips in the same area aboard the Department's research vessel "Emmeline M." during which project personnel pulled their own pots. These trips were made from June 10 through October 30 in 1976 and from June 20 through September 22 in 1977. Unfavorable weather and sea conditions caused the cancellation of several trips scheduled in September and October in 1977. On the 28 trips, 1,962 trap hauls were made and 2,617 lobsters and 3,619 black sea bass (*Centropristis striata*) were caught.

Project personnel measured (to the nearest millimeter) the carapace length of all lobsters caught and recorded the sex, shell condition (hard, soft or "paper shell") and culls (lobsters missing one or both major chelae or having one or both major chelae small and regenerating), as well as the presence or absence of extruded ova on females. The catch was all lobsters in the pots of the fishermen, whereas landings were those kept for sale. The latter was the catch less all ovigerous females, less all sub-legal lobsters

(under 81 millimeters in carapace length) and less those legal-sized lobsters too soft or papery to keep. In addition, all black sea bass caught on all trips were enumerated, and those taken on trips aboard the "Emmeline M." were measured to the nearest 5 millimeters in total length.

A sample of 356 lobsters (291 bought from the commercial fishermen and 65 caught in project gear) of all sizes was taken to the Department's marine laboratory at Flax Pond. These lobsters (103 males and 253 females) were again measured to the nearest millimeter in carapace length and weighed to the nearest 2 grams. After eliminating culls and ovigerous females, the lengths and weights of 88 males and 121 females were used to determine length-weight relationships. The outside width of the second abdominal segment of all females was measured to the nearest millimeter, and the ratio of that width to the length of the carapace, compared with the carapace length, was used as an indicator of maturity as described by Briggs and Mushacke (1979), Krouse (1973), Skud and Perkins (1969) and Squires (1970).

Most of the lobsters taken to the laboratory (103 males and 243 females) were dissected. The gonads, digestive tracts and rectal tissues were preserved in 65 per cent isopropyl alcohol and 35 per cent glycerol for later examination. During dissection and prior to preservation, the color of the ovaries was noted. A dark green ovary or any ovary of non-uniform color showing dark green tissue is indicative of maturity (Krouse, 1973; Lobster Scientific Committee, undated). The ovaries of ovigerous females, although their color was noted, were not used in determining this indicator of maturity. While such specimens are obviously mature, their ovaries are in spent, resting or developing stages and often show no dark green tissue.

Mean ova diameter is another indicator of maturity (Briggs and Mushacke, 1979; Krouse, 1973; Skud and Perkins, 1969; Squires, 1970). Mean diameter was determined, using the method described by Krouse (1973) and Skud and Perkins (1969), by measuring ova removed from the ovaries and magnified at 45× under a dissecting microscope equipped with a micrometer eyepiece. The means for all dark green (or mottled showing dark green tissue) ovaries exceeded 0.80 millimeter, whereas those for all other ovaries were 0.80 millimeter or less. Therefore, the criterion of Skud and Perkins (1969), i.e., a mean ova diameter greater than 0.80 millimeter, was accepted as an indicator of maturity for female lobsters from the inshore waters off the south shore of Long Island. The final indicator used for females was the size of ovigerous individuals measured in the field.

For male lobsters, the presence of sperm in the testes and/or vas deferens, as described by Briggs and Mushacke (1979) and Krouse (1973), was used as an indicator of maturity. The preserved gonads of 103 males were softened by boiling for 15 to 20 seconds in tap water. A smear of the contents was then made on a glass slide and examined for the presence or

absence of sperm at a magnification of 450× under a compound microscope.

Digestive tracts and rectal tissues were examined, both with the naked eye and at a magnification of 45× under a dissecting microscope, for the presence or absence of parasites that according to Uzmann (1970) would indicate whether lobsters had spent time in coastal or offshore waters.

Molt increments were recorded for lobsters that shed either while in the live wells or pots of cooperating fishermen or while being held for dissection in holding tanks at the laboratory.

SIZE AT MATURITY

Size at maturity, particularly for females, was of special interest because of its bearing on fishing regulations.

MALE

Examination of the contents of the testes and/or vas deferens of the male lobsters collected indicated that some reached maturity when 46 to 50 millimeters in carapace length (Table 1 and Figure 2). Most were mature

TABLE 1. PROPORTION, ACCORDING TO 5-MILLIMETER SIZE GROUPS, OF MALE LOBSTERS EXAMINED THAT WERE MATURE BASED ON THE PRESENCE OF SPERM

Size group* (millimeters)	Number examined	Sperm in testes and/or vas deferens		
		Absent	Present	
			Number	Per cent
31-35	1	1	0	0.0
36-40	1	1	0	0.0
41-45	5	5	0	0.0
46-50	6	5	1	16.7
51-55	8	5	3	37.5
56-60	14	2	12	85.7
61-65	15	0	15	100.0
66-70	15	1	14	93.3
71 and over	38	0	38	100.0

*Carapace length.

by the time they reached 56 to 60 millimeters, and only three larger than 55 millimeters in carapace length were immature (one each at 56, 58 and 66 millimeters). Similar results were found in Maine (Krouse, 1973) and western Long Island Sound (Briggs, 1976; Briggs and Mushacke, 1979).

FEMALE

Several criteria or indicators were used to determine size at maturity for the female lobsters collected. All have been found useful and each serves as a check on the others.

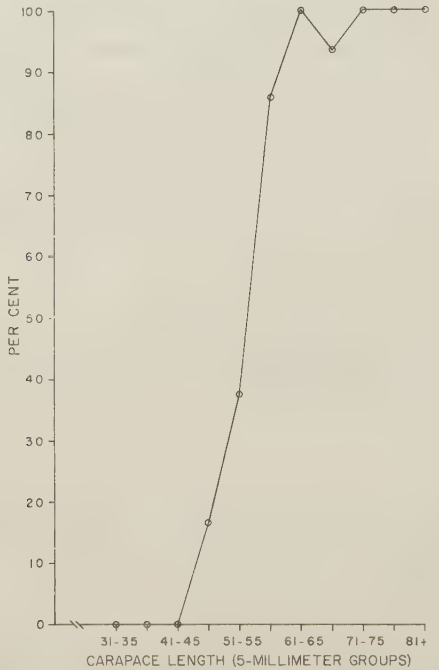

Figure 2. Proportion, according to 5-millimeter size groups, of male lobsters that were mature as evidenced by the presence of sperm in the testes and/or vas deferens.

The ratio of the width of the second abdominal segment to the length of the carapace, compared with the carapace length, has been used by several investigators as a criterion of maturity in female lobsters (Briggs, 1976; Briggs and Mushacke, 1979; Krouse, 1973; Skud and Perkins, 1970; Valenti and Peters, 1977). The data for the specimens from the study area (Figure 3) indicate that a few females may be mature at about 80 millimeters in carapace length. However, nearly all do not reach maturity until they are about 95 to 100 millimeters in carapace length. Conversely, in Long Island Sound nearly all female lobsters were mature by the time their counterparts in the study area were just beginning to reach maturity (Briggs, 1976; Briggs and Mushacke, 1979; Valenti and Peters, 1977).

Ovarian color for non-ovigerous females indicated that few were mature at 81 millimeters in carapace length. However, among those that had reached 86 to 90 millimeters more than half were mature, and all those over 101 millimeters were mature according to this indicator. The mean diameter of ova in the ovaries of non-ovigerous females gave results somewhat similar to those based on ovarian color. Few females smaller than 81 millimeters in carapace length were mature. About half of those from 81 to 90 millimeters in carapace length and all of those over 101 millimeters were mature. The data are shown graphically in Figure 4.

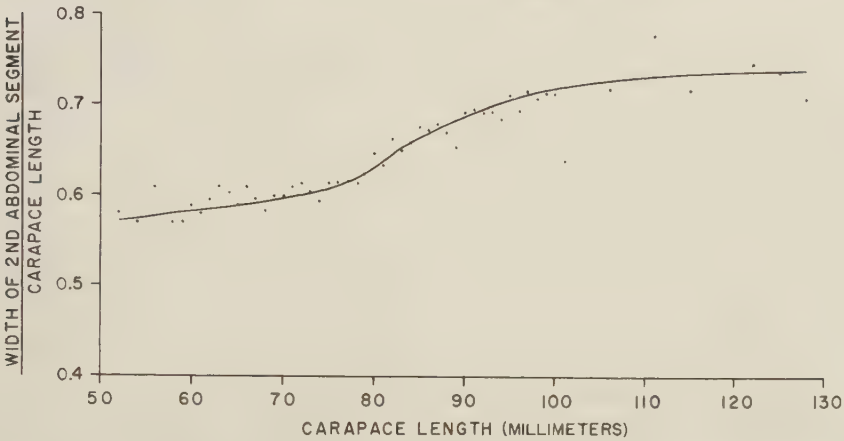

Figure 3. Ratio of the width of the second abdominal segment to the carapace length compared with the carapace length for female lobsters.

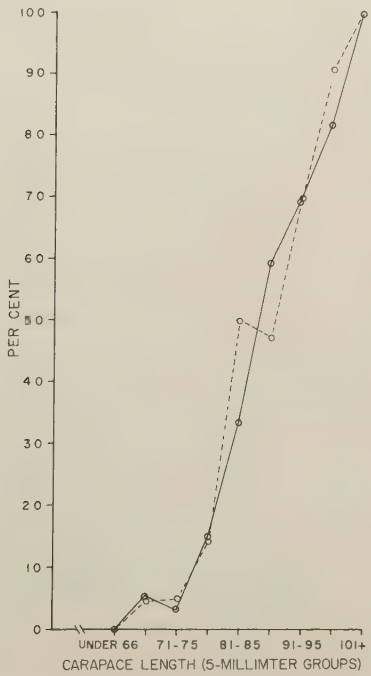

Figure 4. Proportion, according to 5-millimeter size groups, of non-ovigerous female lobsters with dark green (or mottled showing dark green tissue) ovaries (solid line) and with ova diameters greater than 0.80 millimeter (dash line).

The presence of extruded eggs on female lobsters ("berried" or ovigerous females) is obvious evidence of maturity. The 241 ovigerous females examined ranged from 78 to 135 millimeters in carapace length. However,

Table 2. Length-frequency Distribution, According to 5-Millimeter Size Groups, Of Ovigerous Female Lobsters Examined

Size group* (millimeters)	Per cent
76- 80	4.0
81- 85	8.5
86- 90	15.2
91- 95	18.8
96-100	16.1
101-105	17.9
106-110	5.4
111-115	5.8
116-120	2.2
121-125	2.7
126-130	2.7
131-135	0.4
Total	99.7

*Carapace length.

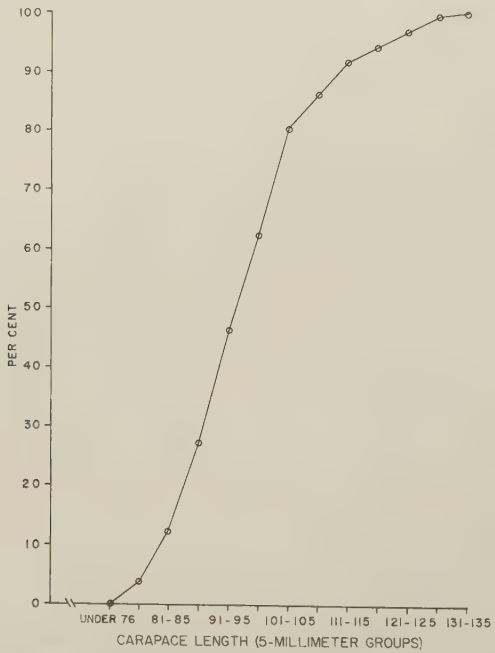

Figure 5. Cumulative percentage, according to 5-millimeter size groups, of female lobsters that were ovigerous.

Table 2 and Figure 5 both show that there were few ovigerous females less than 86 millimeters. It appears, based on this indicator, that most of the female lobsters from the study area do not reach maturity until they are greater than 90 millimeters in carapace length.

All of these criteria showed generally similar results and indicate that, while a very few female lobsters from the inshore waters off the south shore

of Long Island may be mature at 81 millimeters in carapace length, about half do not reach maturity until they reach about 90 millimeters and all are not mature until they exceed 100 millimeters. The results consistently agreed with the findings of Krouse (1973) for Maine and with those of Skud and Perkins (1969) for the waters of the continental shelf off southern New England and New York. They also consistently showed a much greater size at maturity than has been found in other New York waters, i.e., Long Island Sound (Briggs, 1976; Briggs and Mushacke, 1979; Smith, 1977; Valenti and Peters, 1977).

SIZE COMPOSITION

The size composition (by month for the years combined) of the lobster catch in the study area is shown in Figures 6 to 10. The majority ranged between 60 and 139 millimeters in carapace length, although specimens as small as 19 millimeters were caught. There was no pronounced bunching in the pre-recruit (70-80 millimeters) size groups as had been found by Briggs and Mushacke (1979) in western Long Island Sound. Rather, there was a wider, more even spread in the size range. As in western Long Island Sound and other areas (Briggs and Mushacke, 1979; Skud and Perkins, 1969; Zawacki, undated), most (18 of 21) of the largest lobsters (140 millimeters or more in carapace length) were males. Few lobsters caught were smaller than 60 millimeters. This was probably due to gear selectivity and the burrowing habits of small lobsters (Cooper and Uzmann, 1977) rather than being a true picture of the population of small lobsters in the study area.

Male lobsters ranged from 36 to 165 millimeters in carapace length and averaged 83 millimeters. There were 734 males of sub-legal size (less than 81 millimeters or 3 3/16 inches in carapace length) and 591 of legal size caught. Most of the legal-sized males were between 81 and 139 millimeters in carapace length although specimens up to 150 millimeters were not uncommon. Only five exceeded 150 millimeters.

The landings of male lobsters consisted of all the legal-sized males shown in Figures 6 to 10, less seven that were too soft or paper-shelled to keep (one each of 83, 86, 89, 90, 95, 98 and 108 millimeters in carapace length). The average size of the males landed was 98 millimeters.

Female lobsters (including both ovigerous and non-ovigerous individuals) ranged from 19 to 155 millimeters in carapace length and averaged 84 millimeters. There were 690 females of sub-legal size and 833 of legal size caught. Most of the legal-sized females were in the same general size range as the males, but there were fewer large specimens among the females.

The landings of female lobsters consisted of all the legal-sized females shown in Figures 6 to 10, less 232 ovigerous individuals and less nine that were too soft or paper-shelled to keep (one each of 82, 87, 88, 107 and 109

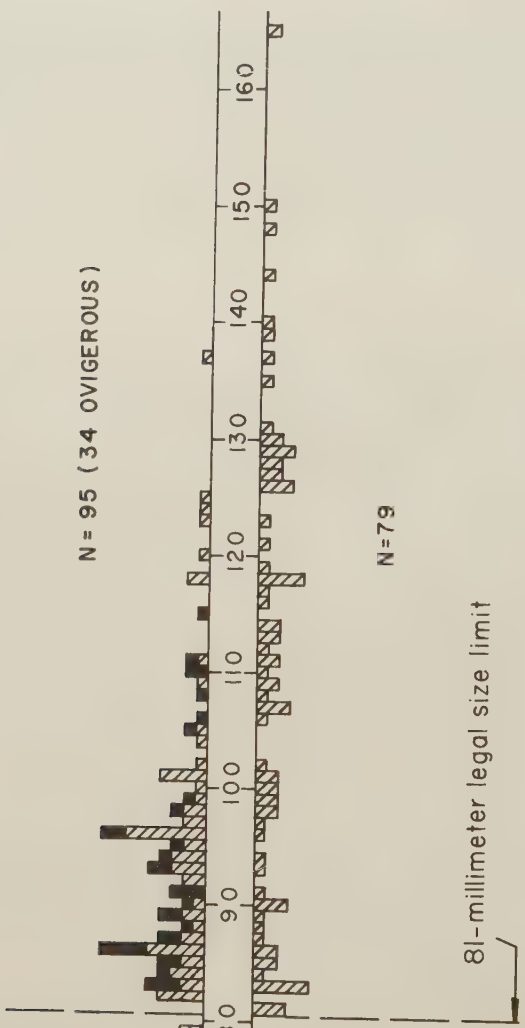

Figure 6. Length frequencies for lobsters caught in June; six trips, 513 traps hauled. Horizontal series of numerals in center denote carapace length in millimeters. Bars above line represent females, below the line males. Solid blocks represent ovigerous females.

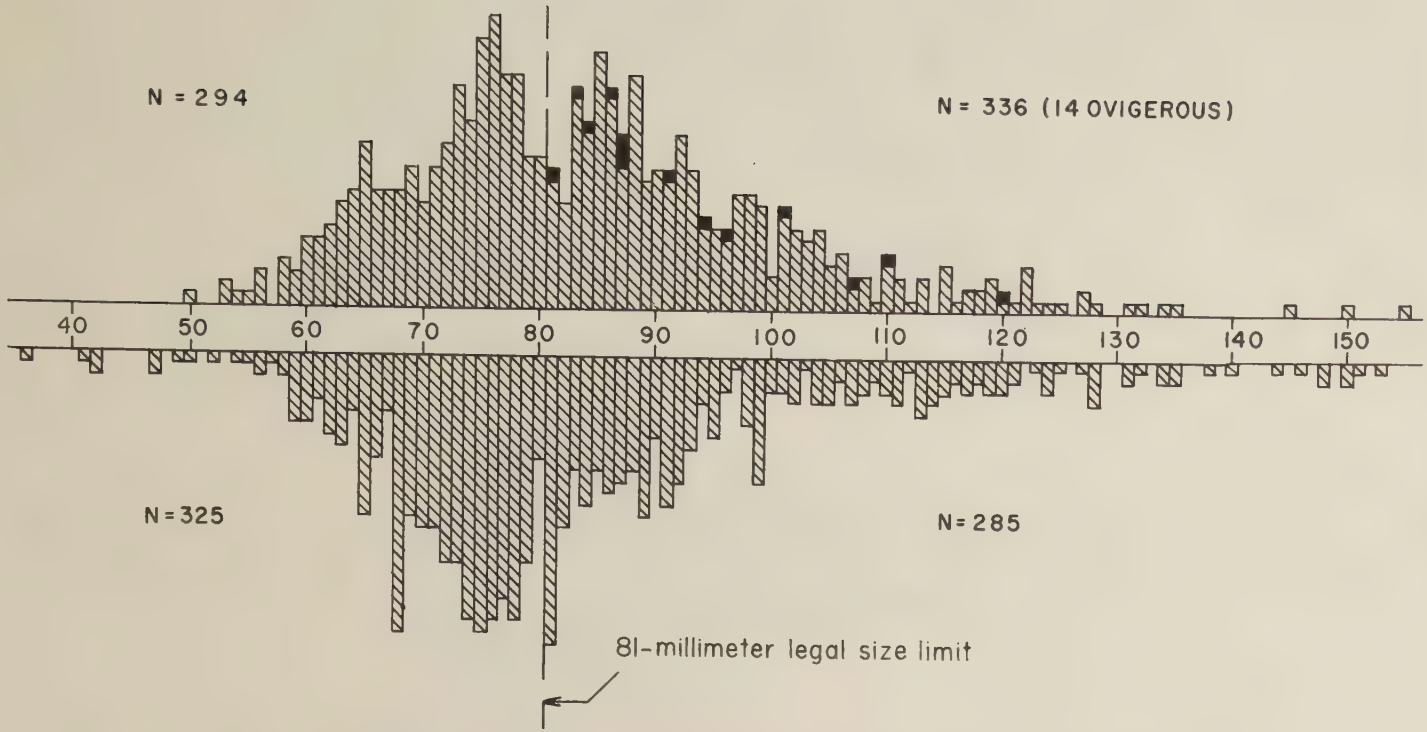

Figure 7. Length frequencies for lobsters caught in July; seven trips, 700 traps hauled. Horizontal series of numerals in center denote carapace length in millimeters. Bars above line represent females, below the line males. Solid blocks represent ovigerous females.

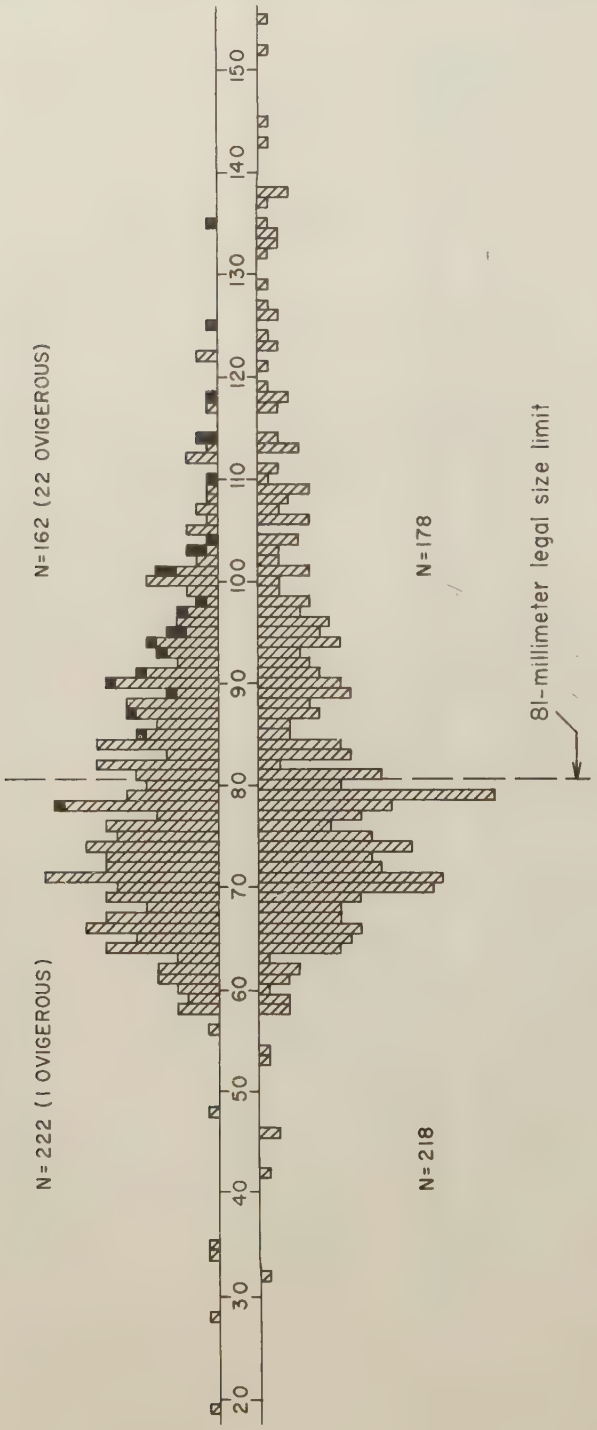

Figure 8. Length frequencies for lobsters caught in August; 10 trips, 410 traps hauled. Horizontal series of numerals in center denote carapace length in millimeters. Bars above line represent females, below the line males. Solid blocks represent ovigerous females.

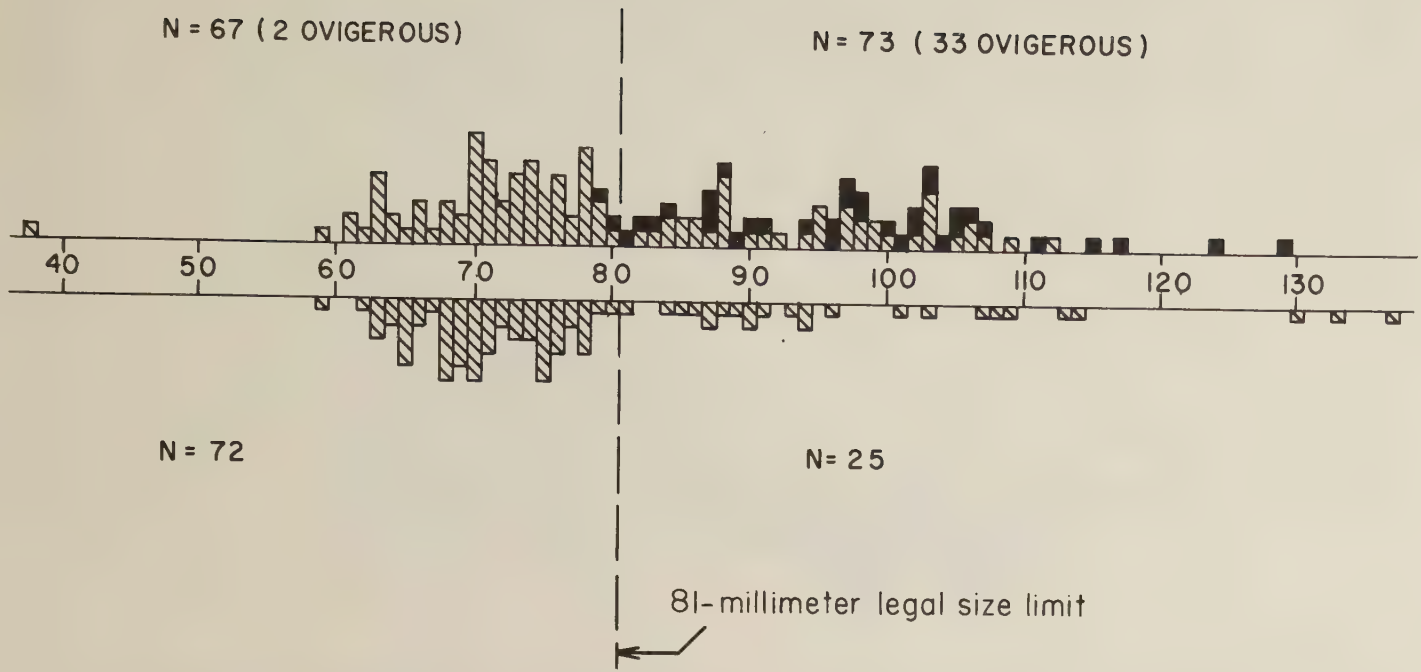

Figure 9. Length frequencies for lobsters caught in September; three trips, 113 traps hauled. Horizontal series of numerals in center denote carapace length in millimeters. Bars above line represent females, below the line males. Solid blocks represent ovigerous females.

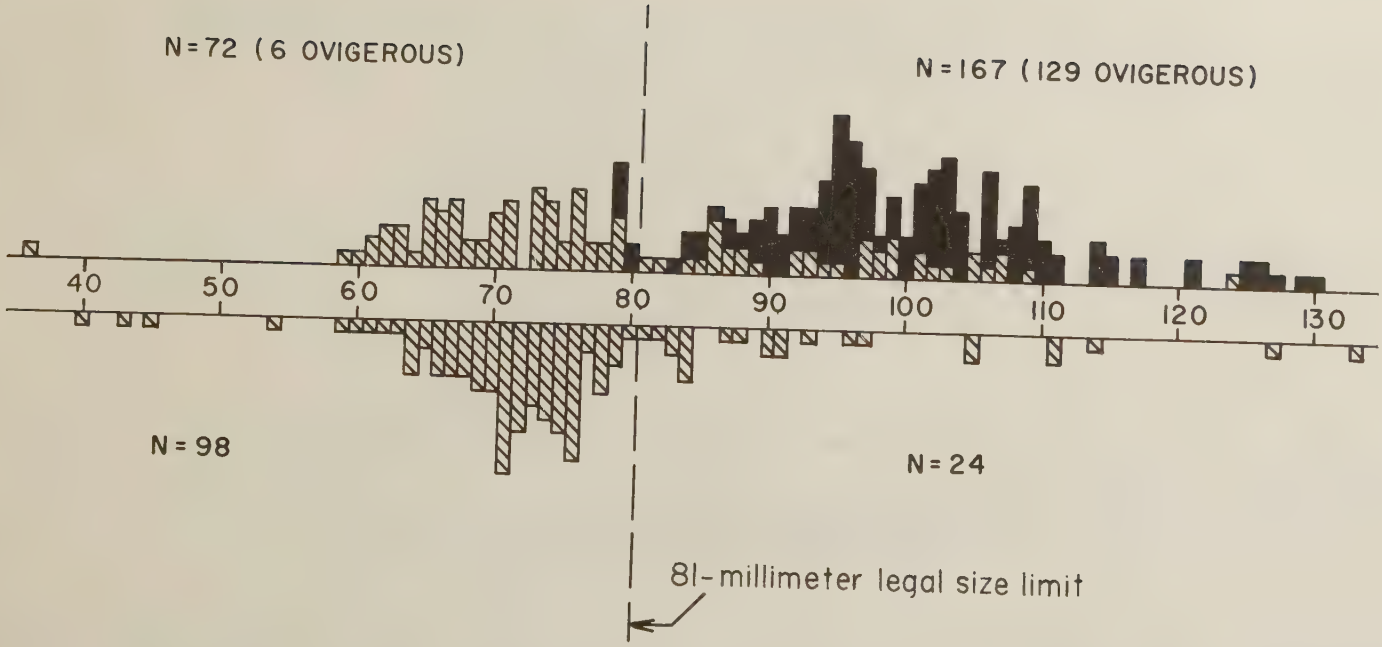

Figure 10. Length frequencies for lobsters caught in October; two trips, 196 traps hauled. Horizontal series of numerals in center denote carapace length in millimeters. Bars above line represent females, below the line males. Solid blocks represent ovigerous females.

millimeters and two each of 85 and 95 millimeters in carapace length). The average size of the females landed was 103 millimeters.

Ovigerous females ranged from 78 to 135 millimeters in carapace length and averaged 99 millimeters. Only nine of the 241 collected were of sub-legal size, most being in excess of 90 millimeters.

The greatest numbers caught and widest size ranges for lobsters of both sexes were recorded in July and August. This tends to strengthen the contention of Cooper (in Briggs and Zawacki, 1974) that most of the lobsters landed from the inshore waters of the south shore of Long Island are migrants from offshore waters. The time of greatest abundance and the size range during that period further support the migratory patterns shown in Cooper and Uzmann (1971, 1977) and Uzmann et al. (1977). Likewise, the size ranges and average sizes were similar to those found by Skud and Perkins (1969) for waters on the continental shelf and canyons off the south shore of Long Island and southern New England. The lobsters collected in the inshore waters off the south shore of Long Island had a wider size range and much larger average size than those from Long Island Sound as recorded by Briggs and Mushacke (1979), Smith (1977), Valenti and Peters (1977) and Briggs (1976).

CULLS

The frequency of culls among lobsters collected in the study area is given in Table 3. For legal-sized specimens, the rate was generally less than 10 per cent. The rates of 13.7 per cent for males and 13.3 per cent for females in August 1976 were probably caused in part by a hurricane that struck the area on August 8-9 of that year. The extremely high rate (40.0 per cent) for legal males in September 1977 is attributable to the small sample of only five specimens for that month. In general, the rates among legal

TABLE 3. PROPORTION (IN PER CENT) OF CULLS AMONG SUB-LEGAL AND LEGAL LOBSTERS FROM THE INSHORE WATERS OFF THE SOUTH SHORE OF LONG ISLAND, 1976-1977

Month	Sub-legal*		Legal	
	Male	Female	Male	Female
1976				
June	9.7	23.3	0.0	7.7
July	10.0	12.3	9.1	6.0
August	27.4	30.2	13.7	13.3
September	39.1	28.4	5.0	5.6
October	37.8	27.8	4.2	4.8
1977				
June	16.7	16.7	4.2	10.7
July	16.0	11.4	6.7	6.4
August	3.5	2.6	3.6	5.8
September	0.0	14.3	40.0	0.0

*Less than 81 millimeters in carapace length.

lobsters were similar to those found by Thomas (1973) for cluster samples of legal lobsters from pounds in Maine. However, they were generally about half or less than those for landed (legal) lobsters observed in western Long Island Sound by Briggs and Mushacke (1979).

The frequency of culls among sub-legal lobsters was generally greater than that among legal-sized lobsters. The effects of the 1976 hurricane apparently lasted much longer among the sub-legal lobsters as evidenced by the high rates (ranging between 27.5 and 39.1 per cent among males and between 27.8 and 30.2 per cent among females) during the period from August to October of that year. That storm did tremendous damage to the pot fishery off the south shore of Long Island and undoubtedly to lobsters caught in the pots. An example was the pot loss observed on board a commercial fisherman's vessel 10 days after the storm. His trawls had been twisted and tangled in almost unbelievable fashion. Some gear was found about 3 kilometers from where it had been set. This fisherman was able to haul only 69 pots that day (normally he hauled more than 100). However, 37 of the pots were damaged beyond repair and the remaining 32 all needed some repair. Quite often only the frame of the pot or a piece of it where it was tied to the trawl was recovered along with torn pieces of funnels and twisted lines.

SEX RATIOS

Sex ratios for the lobsters examined are given in Table 4. Males generally exceeded females in the catch of sub-legal sized lobsters, while the reverse generally held for those of legal size and the total catch of all sizes. In the landings, males exceeded females in June and August, but females predominated in July, September and October. Considering the entire season, there was probably no real difference from a one to one ratio in the number of females per male for the total catch of all sizes (1.13:1) and for the landings (1.01:1).

These data do not show a great dominance of females in the catch and landings as was found in western Long Island Sound by Briggs and

Table 4. Sex Ratios* For Lobsters in the Catch and Landings By Commercial Fishermen in the Inshore Waters Off the South Shore of Long Island§

Group	June	July	August	September	October	Total
Catch						
Sub-legal†	0.85	0.90	1.02	0.93	0.73	0.92
Legal size	1.20	1.18	0.91	2.92	6.96	1.41
Total	1.16	1.03	0.97	1.44	1.96	1.13
Landings‡	0.78	1.13	0.79	1.48	1.58	1.01

*Females per male.
§Data for 1976 and 1977 combined.
†Less than 81 millimeters in carapace length.
‡Legal-sized lobsters less ovigerous females and those too soft to keep.

Mushacke (1979). There does appear to be a similarity to the sex ratios found by Krouse (1973) in Maine waters, by Skud and Perkins (1969) in waters of the continental shelf and canyons off southern New England and Long Island, and by Briggs and Zawacki (1974) at artificial reefs off the south shore of Long Island.

LENGTH-WEIGHT RELATIONSHIPS

Length-weight relationships for 88 male (32-120 millimeters in carapace length) and 121 female (52-128 millimeters in carapace length) lobsters were calculated from the standard equation ($W = cL^n$) using the GM regression described by Ricker (1973) and the logarithms of the weight in grams and the carapace length in millimeters, i.e., $\log W = u + v \log L$. No culls or ovigerous females were included. The resultant equations were:

Male: $\log W = -3.2609 + 3.0913 \log L$

Female: $\log W = -3.2812 + 3.1032 \log L$

Sexes combined: $\log W = -3.2736 + 3.0989 \log L$

Since the calculated weights for males, females and sexes combined for each length category were essentially the same (Table 5), the equation for

TABLE 5. CALCULATED AND OBSERVED MEAN WEIGHTS, ACCORDING TO CARAPACE LENGTH, FOR LOBSTERS FROM THE INSHORE WATERS OFF THE SOUTH SHORE OF LONG ISLAND

Carapace length (millimeters)	Weight (grams)			
	Calculated			Observed
	Male	Female*	Sexes combined	Sexes combined
32	25	. .	25	26
40	49	. .	49	54
50	98	. .	98	104
60	172	172	172	170
70	277	278	278	271
80	419	421	421	425
90	603	607	606	606
100	835	842	840	786
110	1,121	1,131	1,128	. .
120	1,466	1,482	1,478	1,625
128	. .	1,811	1,805	1,726

*In addition there was one female with a carapace length of 52 millimeters and an observed weight of 112 grams.

the sexes combined may be used for lobsters between 32 and 128 millimeters in carapace length from the study area. The relationship is shown graphically in Figure 11. The observed weights generally show close agreement with the calculated weights except for some variation in the larger sizes which may be attributed to small samples in these cases.

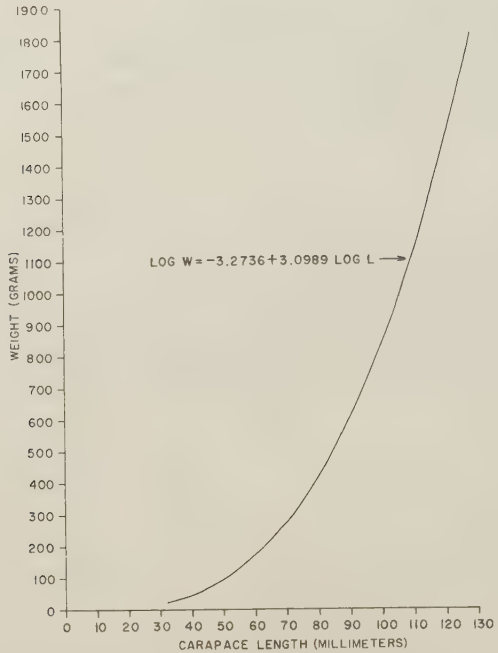

Figure 11. Length-weight relationship for lobsters examined (sexes combined).

PARASITES

Uzmann (1970) indicated that juveniles of an acanthocephalan (*Corynosoma* sp.) were almost exclusively restricted to lobsters from coastal waters; while larvae of a nematode (*Ascarophis* sp.) were almost exclusively limited to lobsters from offshore waters. The acanthocephalan is found encysted on the digestive tract. The nematode is found in the rectal tissues. In the 346 lobsters that were examined during the present study, the acanthocephalan was found in only two (0.6 per cent), while the nematode was found in eight (2.3 per cent). It appears that far more of these lobsters had spent time in offshore waters than had not. These data tend to support the contention of Cooper (in Briggs and Zawacki, 1974) that almost all the lobsters landed from along the south shore are migrants from offshore waters.

TIME OF MOLT AND MOLT INCREMENT

The presence of soft and paper-shelled lobsters in the catch is a good indication of a recent molt. The data recorded (Table 6) indicate that there was no well-defined peak of molting among male lobsters from the inshore waters off the south shore of Long Island. The molt period appears to have been rather evenly spread from June through August. While females may

TABLE 6. PROPORTION (IN PER CENT) OF SOFT AND "PAPER SHELL" LOBSTERS EXAMINED, FOR EACH SEX, 1976-1977

Sex	June	July	August	September	October
Male	1.6	1.0	1.3	0.0	0.0
Female	7.1	1.6	2.5	4.6	0.0

TABLE 7. GROWTH INCREMENT FOR THE FOUR LOBSTERS EXAMINED

Sex	Carapace length (millimeters)		Increase (per cent)
	Pre-molt	Post-molt	
Female	55	65	18.2
Female	63	75	19.0
Male	66	77	16.7
Male	71	83	16.9

molt all summer long, there did seem to be peaks at both the beginning and end of summer.

The data on molt increment were obtained for only four lobsters (Table 7). However, those four showed greater increments than were found by Briggs and Mushacke (1979) for lobsters molting under similar conditions in western Long Island Sound. The increments were close to those reported by Cooper and Uzmann (1971) for lobsters from the continental shelf and canyons off New York and southern New England.

OTHER ASPECTS OF THE FISHERY

The role of the black sea bass, and other fishes and crustaceans, in the commercial fishery for lobsters has never been fully explored. It has long been known that New York's inshore pot fishermen fish for both black sea bass and lobsters using the same gear at the same times and locations. Thus, one cannot categorize them as lobster fishermen or black sea bass fishermen; they are both.

While this study was not designed to cover all the various interrelationships among lobsters and black sea bass, it soon became apparent that the black sea bass were of great importance to the pot fishermen. On the authors' first trip aboard a commercial fishing vessel in the study area, the landings comprised 18 legal lobsters and 691 legal (8 inches, i.e., 203 millimeters, or more in total length) black sea bass. Table 8 shows the monthly landings of both lobsters and black sea bass on all trips (including those of the Department's research vessel). Only in August and September did lobsters outnumber black sea bass in the landings. Figure 12 gives a rough approximation (without set-over days) of the catch per effort for the two species. Figure 13 gives the length frequency of 94 black sea bass caught in project gear. Few were below the legal size limit, and observa-

Table 8. Monthly Landings of American Lobsters and Black Sea Bass Taken By Commercial Pot-fishing Vessels and in Project Gear in the Study Area, 1976-1977

Month	American lobster	Black sea bass
June	139	1,872
July	603	1,192
August	311	282
September	63	30
October	61	241
Total	1,117	3,617

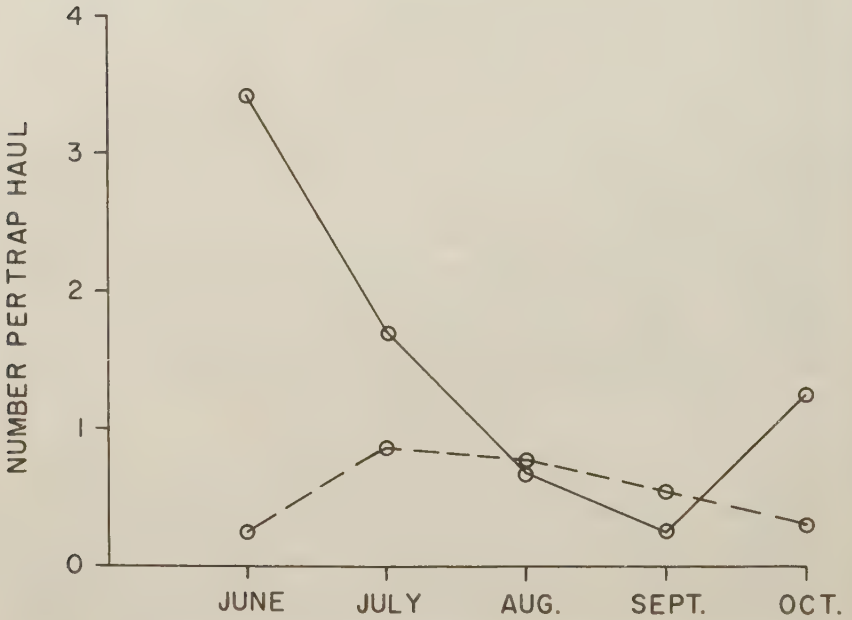

Figure 12. Comparative catch per effort for legal-sized lobsters (dash line) and black sea bass (solid line).

tions indicated that the size composition was similar to that for bass taken by the commercial fishermen. Total New York landings of black sea bass for 1976 and 1977 (Anonymous, 1976, 1977) were 272,274 pounds (worth $99,629) and 231,634 pounds (worth $113,303), respectively. About half of these landings were from inshore pot fishermen (Frederick Blossom, National Marine Fisheries Service, personal communication).

Another animal of rapidly increasing importance to the pot fishery of the inshore waters off the south shore of Long Island is the Jonah crab (*Cancer borealis*). Exploitation of this crab is just beginning. Prior to 1975, none was reported in New York landings (Anonymous 1975, 1976, 1977, 1978). However, from a small catch of 18,000 pounds (worth $5,400) in

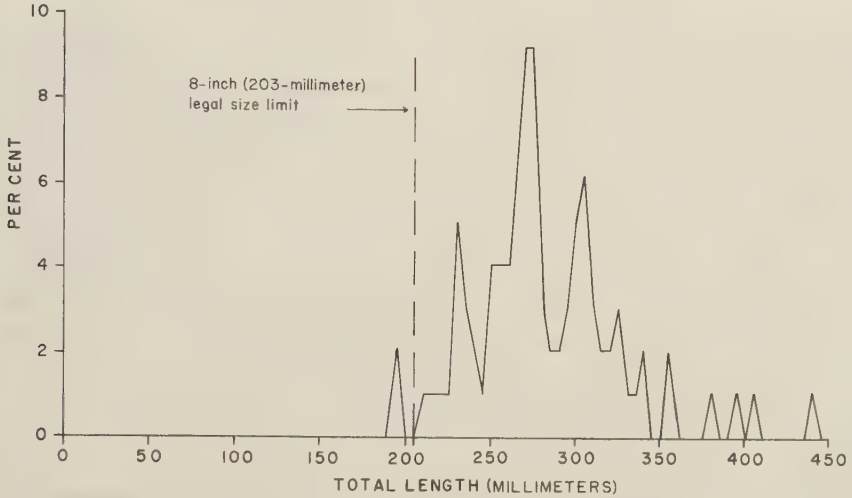

Figure 13. Length-frequency distribution for 94 black sea bass caught.

1975, landings rose sharply to 107,300 pounds (worth $32,190) in 1976 and 285,409 pounds (worth $82,690) in 1977. About half of these landings were from the inshore pot fishery (Frederick Blossom, National Marine Fisheries Service, personal communication). These data, and observations aboard commercial vessels, indicate that the Jonah crab has become an important part of the catch of the pot fishery within the area studied.

Several other species of fish were also taken and landed. These included the conger eel (*Conger oceanicus*), red hake (*Urophycis chuss*) and scup (*Stenotonus chrysops*). None was of great importance. A dozen or so conger eels were usually landed each trip we made on commercial vessels. Whether red hake were kept, discarded or used for bait depended upon the fishermen and current prices. Usually no more than a box (about 45.5 kilograms) or two was landed on any trip. Scup were occasional catches, rarely more than a dozen fish a day.

Among the fish caught and discarded, the ocean pout (*Macrozoarces americanus*) and sea raven (*Hemitripterus americanus*) were the most common. Other discards included tautog (*Tautoga onitis*), cunner (*Tautogolabrus adspersus*), spotted hake (*Urophycis regius*), fourspot flounder (*Paralichthys oblongus*), lined seahorse (*Hippocampus erectus*) and spider crabs (*Libinia* spp.). Only the ocean pout and sea raven were taken in sufficient numbers to offer any potential to the fishery, were they marketable.

DISCUSSION

American lobsters taken in the inshore waters off the south shore of Long Island show a marked affinity with lobsters found on the continental

shelf and canyons off southern New England and New York. The size at maturity of females, size composition of catches and landings, sex ratios and times of great abundance (strongly indicative of migratory behavior), as well as the parasites present, all are evidence that these lobsters are of the same stock as "offshore lobsters". Indeed, studies of the migrations of "offshore lobsters" show a definite seasonal movement to inshore waters by part of that group (Cooper and Uzmann, 1971, 1977; Uzmann et al., 1977). The authors believe that no distinction can be demonstrated between "inshore lobsters" and "offshore lobsters" off the south shore of Long Island. For management purposes, this is advantageous because any measures applied to one group would have an effect on the other. On the other hand, the evidence strongly suggests that these oceanic lobsters are distinct in size at maturity and movements from the lobsters in Long Island Sound (Briggs and Mushacke, 1979; Lund et al., 1970; Valenti and Peters, 1977).

In both the Sound and waters off the south shore of Long Island, male lobsters mature at a smaller size than females, almost all being mature by the time they reach 56 to 60 millimeters in carapace length. This creates no problems with mating, since males can successfully copulate with females twice their bulk (Hughes and Mattheissen, 1962). On the other hand, although in Long Island Sound most females are mature at about 80 millimeters, in waters off the south shore few mature at this size and only about half are mature at 90 millimeters in carapace length. This disparity for the females in the two areas is significant with respect to setting proper size limits for the commercial fishery.

The minimum legal size currently [1979] in effect in New York is 3 3/16 inches (81 millimeters) in carapace length. Although data for lobsters in Long Island Sound indicate that this does not impair reproduction there (Briggs and Mushacke, 1979), the findings of the present study indicate that such is not the case with respect to waters off the south shore of Long Island since few female lobsters there reach maturity at that size. For these waters, a more desirable limit (biologically) would be 3 1/2 inches (89 millimeters) as has been proposed by the Lobster Scientific Committee (1974) and the Northeast Marine Fisheries Board (1978). This would allow about half the females to reach maturity and result in a greater yield per recruit (greater poundage of lobster harvested) for the fishermen.

The management plan recommended by the Northeast Marine Fisheries Board (1978) also proposed that each lobster trap be provided with a rectangular escape vent 1 3/4 x 6 inches (44 x 152 millimeters). Several studies in Maine, Massachusetts and Rhode Island (Fair and Estrella, 1976; Fogarty and Borden, undated; Krouse, 1978; Krouse and Thomas, 1975; Nulk, 1978; Pecci et al., 1978) have shown that vents of this size allow the escape of sub-legal lobsters and often significantly increase the catch of legal lobsters. However, such vents also allow the escape of black sea bass

and Jonah crabs, an undesirable feature for Long Island fishermen. A suggested alternative, a round escape vent 58 millimeters (2.28 inches) in diameter, has been used in Maine and Rhode Island and found effective in retaining Jonah crabs and legal lobsters while reducing the catch of sublegal lobsters (Fogarty and Borden, undated; Krouse, 1978).

Retention of black sea bass by the two styles of vents has not been fully explored. Indeed, in some areas, these fish may not be wanted in pots because of their known predation upon lobsters trapped in them (Pecci et al., 1978). However, they are desired and are an important phase of the pot fishery in the inshore waters off the south shore of Long Island. There is some evidence that black sea bass have a body depth to length ratio of 3.7 to 1 (Thomas D. Morrissey, National Marine Fisheries Service, personal communication). Thus, theoretically, the proposed round vents would retain bass 214 millimeters or more in length. However, this would probably allow between 10 and 20 per cent of the legal catch to escape. More study of escape vents and their effect on the catch of black sea bass would be needed to assess their usefulness in the pot fishery in the inshore waters off the south shore of Long Island.

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MOVEMENT OF THE RED FOX IN CENTRAL NEW YORK[1]

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ABSTRACT

Red foxes were captured by den excavation and trapping on a 100-square-mile study area in Cayuga County, New York, during the years 1972 to 1977. Each was tagged and released at the capture site. A total of 551 pups and 85 adults were tagged. Recovery records were obtained both from animals taken during continued project operations and from carcasses of tagged foxes taken by private trappers or found dead. The data were analyzed to indicate the number and distribution of red fox families on the area from year to year and the movement of individuals, especially pups. During the six years the number of families fluctuated from 21 to 28. Most of the pups rehandled during the summer had ranged less than 0.7 mile from where they had been originally captured. About two-thirds did not range over 0.3 mile, indicating a home range of not over 0.28 square mile. There was no evidence of a lack of suitable den sites or other habitat deficiency, but 34 per cent of all the foxes captured appeared to have shared their home range with members of other red fox families and communal denning was frequent. Pups gradually dispersed from parental home ranges from October through January, males usually travelling farther than females. The distances travelled by dispersing pups and adults in the present study were considerably shorter than those reported for the red fox in the midwestern United States but were comparable to earlier records from central New York as well as to data from the United Kingdom and Scandanavia.

The State Departments of Environmental Conservation and Health have cooperated since the 1940's in efforts to control the spread of rabies in wildlife in New York (Linhart, 1960; Parks, 1968). The primary method used has been reduction of local population densities of the red fox (*Vulpes fulva*) and gray fox (*Urocyon cinereoargenteus*) by trapping in zones. Expressing dissatisfaction with the effectiveness of trapping for this purpose, Parks (1968) discussed poison (Cyanogas), disease (sarcoptic mange) and chemical reproductive inhibitors as alternatives.

Investigation of reproductive inhibitors indicated that Quinesterol, potentially the most effective compound, was also hazardous (Tullar, 1973). Many small mammals and some birds were found to be more likely

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[1]The authors depended heavily upon the goodwill and cooperation of most of the landowners in the Cayuga County Towns of Brutus, Cato, Conquest, Mentz, Sennett and Throop. Many trappers, hunters and fur dealers in Cayuga, Onondaga, Oswego, Seneca and Wayne Counties provided information about tagged foxes at their own expense. Environmental Conservation Officers E. M. Lamphere, M. L. Mobbs, W. Hasenjager, G. K. Viele and C. M. Gay also provided support. Special thanks are due Ernest Saggese (deceased), Stewart Van Wie, Cecil Barrett, Delmer Stalnaker, Allan Martel, Howard Parish and Elmer Davies who trapped and tagged most of the foxes discussed. Among other Department personnel: E. J. Parks and G. H. Teidman helped plan the study and choose the study area; John Proud, Richard Loveless (deceased) and Dale Smith cooperated in providing the Howland Island Game Management Area as a base of operations; and Gary Parsons, Nathaniel Dickinson, Mark Brown, Albert Koechlein, Bruce Penrod and George Mattfeld reviewed the manuscript.

than foxes to consume treated baits. Winkler et al. (1975) developed an oral anti rabies vaccine for dispersal in treated baits. This approach was also questioned since treated baits are not selective and the method has an unacceptable potential for introducing rabies among wildlife. It was evident that a better understanding of fox behavior, movement and population characteristics was needed for management and disease control efforts to be effective in the State. Therefore, a study of foxes on an area in central New York was undertaken in June 1972. The objectives included development of methods for capturing, tagging and censusing foxes and determination of patterns, periods and distances of fox movement. This paper presents the findings that relate to red fox movement.

THE STUDY AREA

The study area was an arbitrarily chosen 10-mile square[2] in northcentral Cayuga County some 20 miles west of Syracuse. It comprises part of the Erie Ontario Lake Plain physiographic province and is covered with large, broken, north-to south oriented ridges of drumlins (Hutton, 1971). The broad valley of the Seneca River divides it into two nearly equal hilly portions. Drumlins rise 325 feet above the river in the southeastern part of the area and to 225 feet in the northern part. Most of the streams flow north or south to the Seneca River.

The temperature range in central New York is less than that in the central United States because of the influence of Lake Ontario. For Cayuga County, records of the U.S. Weather Bureau show that summer temperatures reach 90° F for three to 15 days during the period from June through September, while winter temperatures drop to 0° F. or lower for three to 14 days during the December through February period. Precipitation ranges from 21 2 to 42.2 inches annually, and 75 to 100 inches of snow falls each winter (A. B. Peck, in Hutton, 1971).

Although 60 per cent of Cayuga County has been classified as farmland, there is a growing population of rural non-farm residents. The average farm size was 202 acres in 1974 when approximately 110 people per square mile resided in the county (Anonymous, 1977). There were few fields of 80 acres or more on the study area, most being 20 acres or less (Figure 1). The comparatively small fields, numerous brushy hedgerows, stone piles and encroaching woodlot borders provided a complex interspersion of cover types and a wide variety of fox prey species. Based on an inventory of land use and natural resources in the State by the Office of Planning Services (Anonymous 1972), the area in 1970 comprised: plantation, brushy and mature forest lands (22.7 per cent); inactive agricultural, plowed in rotation or permanent open lands (58.6 per cent); wooded and marshy

[2]Depicted in the southeastern corner of the 15-minute U.S.G.S. Weedsport (N.Y.) quadrangle (N4300-W7630, 1954).

Figure 1. A representative portion of the study area. (approximate scale: 1 inch = 0.7 mile)

wetlands (12.4 per cent); lakes, ponds, streams and rivers (1.4 per cent) and residential areas, highways and railroads (4.9 per cent).

METHODS

Data were gathered from 1972 to 1977 by capturing, tagging and releasing foxes on the study area and in the vicinity and recording subsequent observations of the tagged animals.

CAPTURING AND TAGGING FOXES

Searches for fox sign (Scott, 1943) were made with permission of the landowners. Foxes were trapped with No. 1 1/2 double coil spring leg

hold traps (Oneida-Victor) which had been modified by covering the jaws with polyethylene tubing, shortening the chains to 10 inches and fitting each chain with an additional swivel. The traps were deployed in "dirt hole" sets (Seagears, 1944). Commercial bait, lure and red fox urine were used as attractants. Also, beginning in 1973, red foxes were captured from late March through early June by excavating their dens as described by Berchielli (unpublished).

Red fox pups were distinguished from adults through August by differences in body size and coat development as described by Fisher (1951). During September and early October, however, tooth development (Sheldon, 1950) and coat condition (Linhart, 1968) were used as criteria.

Foxes were restrained for tagging with catch loops, gloved hands and wire netting. Both ears of all foxes were tagged. An individual number and the letters "ENCON" were stamped on each tag. Two types were used. Very small pups were marked with 10-millimeter-square, tack-shaped, aluminum or monel "rabbit" tags which were fastened through a single hole in each ear to a 15-millimeter washer.[3] Larger pups and all adults were marked with 5 x 20-millimeter brass wing tags (Ketchum Co., Lake Luzerne, N.Y.) which were fastened through two holes in each ear so that the tag did not extend over the edge and the locking parts were protected by the concave part of the ear. All foxes were released at their points of capture as soon as possible after being tagged.

Although tagged foxes were inadvertently recaptured during den excavation and trapping, no special effort was made to follow tagged families and recapture them. Den sites of pups captured in April and May were usually avoided during trapping in June and July in an effort to locate all red foxes on the study area. Unless recaptured foxes were injured or extremely mangy, they were released as soon as they were identified.

Obtaining Fox Carcasses

Efforts were made, during all seasons of the year, to obtain the carcasses of all foxes found dead or killed on or near the study area, and project personnel asked about such specimens whenever they met residents or sportsmen. To avoid repetitious explanation and to serve as a constant reminder, each person was given a small leaflet listing the objectives and purposes of the study and the telephone numbers of resident project personnel. News releases were made to local newspapers each fall to promote public awareness of the possibility of taking tagged foxes. Fox trappers, hunters and local fur dealers were contacted periodically during each fall and winter to obtain a sample of fox carcasses. Annual meetings were held with the New York State Trappers Association and the Raw Fur Dealers

[3]Use of these rabbit tags was discontinued after 1975 and all tagging was done with the brass wing tags.

Association to report the progress of the study and to solicit continued cooperation. A combination of advertisements in four area shopping guides and a telephone answering service were also used to obtain carcasses. No rewards were offered.

Each fox carcass was examined for evidence of reproductive status, diseases and parasites, trap damage and the cause of death. During each autopsy, a premolar tooth was extracted. These teeth were processed, sectioned, mounted and stained following the methods of Stone et al. (1975), and age was determined by counting the cementum layers as described by Monson et al. (1973).

RECORDING NUMBERS AND MOVEMENTS OF FOXES

Since the study area was a 10-mile square, it was first divided into 100 square-mile sections for recording observations. East-west tiers of sections were designated by letter, and north-south tiers by number, so that each section could be identified by its coordinates. Then, for more precise plotting of data, each section was subdivided into quarter-sections (i.e., NE, SE, SW and NW) and each of these in turn into 40-acre units similarly designated—a total of 16 units per section. Thus, an observation might be recorded as having been made in the SW "40" of the NE quarter-section of Section B-5.

Scott (1943) observed that red fox families are coherent groups from March to October each year and occupy one or more identifiable burrows from March to June. Thus, evidence from den searches in the spring and from captures of pups and adults in the summer could be used to indicate the number of families on the study area and their home ranges. Families were identified from the capture records for individuals. A family was usually associated with a known den and was recorded under the section in which the den was located. When a den was not found, groups that included pups and that were captured, and often recaptured, in the same general vicinity were considered families. If, in such cases, the points of capture involved more than one section, the family was recorded under the one in which the majority of the captures occurred. Families occupying sites outside the study area, but in the vicinity, were also recorded. The methods of Freeman (1953) were used to analyze the pattern of spacial distribution of red fox families.

Movements of tagged foxes were determined by measuring straight lines plotted between the points of initial capture and subsequent rehandling in each case. In a few instances the exact location was not clear, and the measurement was made to the center point of the "40" involved. For tagged foxes that had left the study area, capture points were usually reported with reference to the nearest road intersection, and other observations outside the area were similarly reported. For analysis of pup movements, the distances and directions between the points of original capture and those

where the pups were subsequently rehandled were plotted to scale with reference to a hypothetical common original capture point as described by Tester and Siniff (1965). In order for these to be comparable, the direction of movement as mapped was plotted as its azimuth measured from due north to the nearest 10 degrees. A hypothetical geographic center of pup activity was then computed by the method of Hayne (1949).

For the red fox pups he tagged, Jensen (1973) considered the greatest distance moved by any of those rehandled before the end of their first September to have been the criterion of the minimum dispersal distance. This approach was also used in the present study. Dispersal of adults was assumed to have been similar to that of pups, but there was no evidence to support this assumption, and some pups may have used the home ranges of several adult females.

RESULTS AND DISCUSSION

It is felt that a very large proportion of the red foxes on the study area during the period of this study were captured and tagged and that injuries were minimal. Analysis of the data collected provides important information concerning the ecology and behavior of the species on range such as that in central New York.

Foxes Tagged and Subsequent Records

During the six years of the study, there were 636 instances in which red foxes were tagged and released. These are summarized in Table 1 according to the method of capture and the age of the animals involved. For foxes dug from dens (primarily in the spring) the ratio of pups to adults was 255 to 9 (28:1), while for those trapped (chiefly during the summer) it was 362 to 80 (4.5:1). With respect to these figures, the instances in which foxes were first captured by den excavation and later rehandled by trapping by project personnel were included in both ratios on the assumption that the original handling had not biased their susceptibility to being trapped.

Storm et al. (1976), who trapped red foxes at dens in Iowa and Illinois, reported a ratio of 1.987 pups to 62 adults (32:1). Jensen (1973), trapping at dens in Denmark, captured 460 pups and 16 adults (27:1). Neither of these ratios was significantly different ($P < 0.05$) from that for foxes taken at dens during the present study.

However, the difference between the age ratio for foxes dug from dens in the spring and that for foxes trapped during the summer was highly significant ($P < 0.01$). This difference reflects the tendency of adult males to be absent from dens where pups were present and a tendency of vixens to be present for only brief periods when nursing pups. After leaving the den in June, pups and adults were somewhat more likely to occur together. Also,

the 4.5:1 ratio of pups to adults was significantly greater ($P < 0.05$) than the ratio of 3.2:1 for mean placental scar counts in the Lake Plain region as indicated by the data reported by Layne and McKeon (1956).[4] That the actual ratio observed was higher than that based on placental scars suggests that, through the summer, some adults continued to avoid groups of pups or were more difficult than pups to trap. However, it is doubtful that it was the result of adults learning to identify and avoid traps.

Table 1 summarizes the foxes tagged, according to the method of capture and age, and the recoveries[5] recorded. The recovery rate for red foxes

TABLE 1. NUMBER OF RED FOXES TAGGED, ACCORDING TO METHOD OF CAPTURE AND AGE, AND PROPORTION RECOVERED

Item	Method of capture								Total	
	Den excavation		Den excavation and trapping*		Trapping		Taken from captivity			
	Pup	Adult	Pup	Adult	Pup	Adult	Pup	Adult	Pup	Adult
Number tagged	185	5	70	4	292	76	4	0	551	85
Recovered§										
Number	59	4	19	2	102	22	0	0	180	28
Per cent	32	80	27	50	35	29	. .	. .	33	33

*Represents foxes first captured by den excavation (at which time they were tagged) and later trapped and released by project personnel

§Represents tagged foxes taken by fur trappers or found dead or moribund.

tagged as pups was the same as that for adults (33 per cent). The proportion of the tagged foxes recovered tended to increase with time for pups but not for adults (Table 2). The recovery rates for pups, in the year they were trapped, ranged from 17 to 31 per cent and averaged 22 per cent, while in the second and third years they were 10 and 4 per cent, respectively.

Pups initially dug from dens were not recovered at a significantly different rate from those that had been trapped. Of 185 originally dug from dens and never trapped by project personnel 32 per cent were recovered, while for 292 pups originally trapped 35 per cent were recovered. Among 160 tagged red foxes trapped for fur during or after their first open season, there was no significant difference in the proportion that had been dug from dens and that had been trapped.

However, for pups tagged on the study area, the proportion recovered (29 per cent) was significantly ($P < 0.01$) lower than that (45 per cent) for

[4]Layne and McKeon reported a mean of 6.4 placental scars per female. Assuming equal numbers of each sex among the adult foxes, this would represent an age ratio of 3.2:1.

[5]In this study, a recovery was considered to mean a dead fox, i.e., one either taken by a fur trapper or found dead. It does not include animals rehandled and released by project personnel.

Table 2. Proportion of Tagged Red Foxes Recovered, According to Number of Years After Release

Year	Number tagged	Number recovered, by year after release						Total	
		1	2	3	4	5	6	Number	Per cent
Pup									
1972	17	5	2	1	0	0	1	9	53
1973	71	22	5	3	2	1	xx	33	46
1974	148	33	13	3	5	xx	xx	54	36
1975	179	30	10	4	xx	xx	xx	44	25
1976	74	20	7	xx	xx	xx	xx	27	36
1977	62	13	xx	xx	xx	xx	xx	13	21
Total	551	123	37	11	7	1	1	xx	xx
Tagged pups available*		551	379	295	149	48	9	xx	xx
Tagged pups recovered									
Number		123	37	11	7	1	1	xx	xx
Per cent		22	10	4	5	2	11	xx	xx
Adult									
1972	13	3	3	0	0	0	0	6	46
1973	11	0	2	1	0	0	xx	3	27
1974	16	3	2	1	0	xx	xx	6	38
1975	31	1	5	2	xx	xx	xx	8	26
1976	7	1	0	xx	xx	xx	xx	1	14
1977	7	4	xx	xx	xx	xx	xx	4	57
Total	85	12	12	4	0	0	0	xx	xx
Tagged adults available*		85	70	52	25	15	7	xx	xx
Tagged adults recovered									
Number		12	12	4	0	0	0	xx	xx
Per cent		14	17	8	0	0	0	xx	xx

*All the foxes tagged during the six years represented the total available for recovery during the first year after release. For the second year, the total available represents the sum of those tagged through 1976 less all first-year recoveries through that year. For the third year, the total available represents the sum of those tagged through 1975 less the aggregate of first-year and second-year recoveries through that year . . . and so on.

those that had been tagged outside the area. A probable explanation for this was that pups tagged on the study area were usually found by project personnel without assistance. Pups tagged off the area, in contrast, were usually from families reported to project personnel by landowners or sportsmen and known to the interested public including local trappers. The greater degree of recovery of such pups also indicates that they had remained in the vicinity of their dens into the trapping season despite some harassment by the public in addition to having been captured and tagged.

Prior to their discontinuance, rabbit tags were used to mark 101 small pups dug from dens in early April, and 31 pups that were losing or had lost these tags were recaptured during the summers of 1974 and 1975. These pups were retagged with brass wing tags which brought the total so tagged to 481 and reduced the total marked with rabbit tags to 70. By December 1, 1977, recoveries totalled 167 (35 per cent) for the pups marked with wing tags but only 16 (23 per cent) for those marked with rabbit tags. Since it was probable that about half of the pups marked with

rabbit tags had lost their tags, it was fortunate that the opportunity had been taken to retag those that were recaptured.

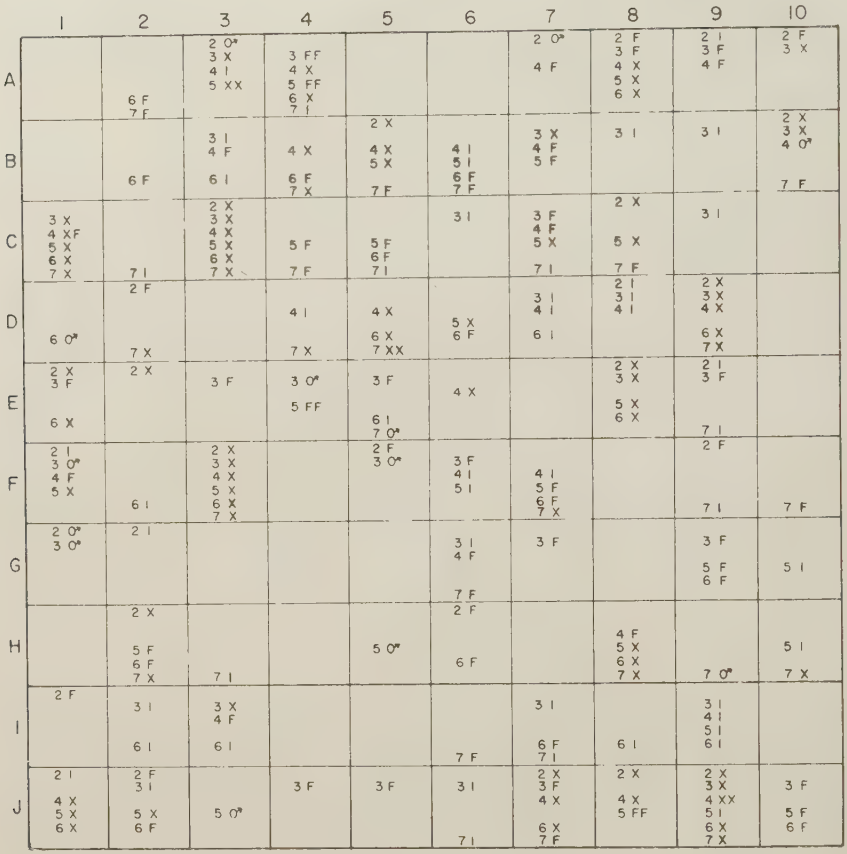
SPRING AND SUMMER POPULATIONS AND RANGE

There were 151 red fox families identified on the study area — 21, 27, 25, 28, 26 and 24, respectively, for the years 1972 to 1977. However, the annual fluctuation in the number of individuals was much greater than that in the number of families. The distribution of the families on the area from year to year according to the section with which they were primarily associated is shown in Figure 2. Except during 1975 when it fell within the range that would have occurred at random (as determined after Freeman, 1953), the incidence of two families concurrently occupying the same section was less than would have been expected if they had been randomly distributed. Except in 1973 and 1976 when it was lower, the incidence of families concurrently occupying adjacent sections (including diagonals) was also in the range that would be expected to have occurred by chance. The data for 1973 and 1976 suggested that some families may have avoided others in these years. During the study, there was no evidence that red fox families were attracted to others, except with respect to communal denning.

For the red fox pups that were tagged, 290 recaptures and recoveries involving 272 individuals were recorded. The corresponding figures for adults were 31 and 29, respectively. The movements of these animals are summarized in Tables 3 and 4. In a case which also was evidence of communal denning, two families dug from dens and tagged in April were again taken by digging in early May. Tagged pups from both families were found sharing dens with unmarked family members 0.3 and 0.5 mile from the dens where they were first captured. Of 137 pups rehandled from April through September of their first year, only one (recaptured in September) had moved as far as 1.5 miles. The average monthly movement from June through September varied from 0.2 to 0.5 mile. The pattern of spring and summer movement (Figure 3) indicated no tendency for pups to move in a consistent direction.

For pups rehandled during their first summer, 64 per cent had not moved more than 0.3 mile and 94 per cent had not moved more than 0.7 mile from their original capture points (Figure 4). Movements of over 0.3 mile did not appear to have been the result of increased cruising radii but seemed to represent changes in the centers of pup activity. After establishing independent activity centers, pups seemed to range 0.2 mile or less about them for the rest of their first summer. The recapture points for two family groups of pups, plotted in Figure 5, illustrate probable changes in activity centers and reduced cruising radii among the pups afterward.

Similar changes in the activity centers of red fox families were reported by Scott (1943) who found that three families moved from 0.1 to 0.8 mile


1 2 3 4 5 6 7 8 9 10
A
2 O* 3 X 4 I 5 XX
3 FF 4 X 5 FF 6 X 7 I
2 O* 4 F
2 F 3 F 4 X 5 X 6 X
2 I 3 F 4 F
2 F 3 X
6 F 7 F
B
3 I 4 F 6 I
4 X 6 F 7 X
2 X 4 X 5 X 7 F
4 I 5 I 6 F 7 F
3 X 4 F 5 F
3 I
3 I
2 X 3 X 4 O* 7 F
C
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5 F 6 F 7 I
3 I
3 F 4 F 5 X 7 I
2 X 5 X 7 F
3 I
7 I
D
2 F 7 X
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4 X 6 X 7XX
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3 I 4 I 6 I
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2 X 3 X 4 X 6 X 7 X
6 O*
E
2 X 3 F 6 X
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3 O* 5 FF
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6 I
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2 F 3 O*
3 F 4 I 5 I
4 I 5 F 6 F 7 X
2 F 7 I
7 F
G
2 O* 3 O*
2 I
3 I 4 F 7 F
3 F
3 F 5 F 6 F
5 I
H
2 X 5 F 6 F 7 X
7 I
5 O*
2 F 6 F
4 F 5 X 6 X 7 X
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7 O*
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5 O*
3 F
3 F
3 I 7 I
2 X 3 F 4 X 6 X 7 F
2 X 4 X 5 FF
2 X 3 X 4 XX 5 I 6 X 7 X
3 F 5 F 6 F

KEY

2-7	last digit of the years occupied
X	one family occupying a den
XX	two families occupying the same den
F	one family (no den located)
FF	two families (no den located)
XF	two families (only one den located)
O*	no family, but adult male present
I	no family, but individual(s) present from adjacent family

Figure 2. Distribution, over the 100 square-mile sections of the study area, of the 151 red fox families recorded during the denning and rearing seasons of 1972 to 1977.

and used three to seven dens from April through June. Sheldon (1950) reported three moves of a single red fox family in May, and Rue (1969) observed a red fox family that moved 11 times in a 3-month period in the

TABLE 3. MEAN DISTANCE MOVED BY RED FOX PUPS BETWEEN TIME OF TAGGING AND REHANDLING

Interval	Female					Male					Total rehandled
	Number rehandled	Distance moved (miles)		Dispersed§		Number rehandled	Distance moved (miles)		Dispersed§		
		Range	Mean	Number	Per cent		Range	Mean	Number	Per cent	
April	4	0.3	0.3	0	. .	2	0.3	0.3	0	. .	6
May	3	0.0- 0.5	0.3	0	. .	5	0.0- 0.5	0.4	0	. .	8
June	2	0.1- 0.4	0.2	0	. .	2	0.1- 0.3	0.2	0	. .	4
July	13	0.1- 1.3	0.4	0	. .	14	0.1- 1.3	0.4	0	. .	27
August	42	0.1- 0.7	0.3	0	. .	26	0.1- 0.7	0.3	0	. .	68
September	9	0.1- 1.2	0.4	0	. .	15	0.1- 1.5	0.5	0	. .	24
First summer	73	0.0- 1.3	0.35	0	. .	64	0.0- 1.5	0.38	0	. .	137
October 1-15	9	0.2- 3.7	1.0	2†	22	8	0.1-12.2	1.8	1	12	17
16-31	12	0.2- 6.0	1.8	3	25	24	0.1- 9.0	3.1	13	54	36
November	10	0.2- 5.8	1.3	3	30	13	0.1-23.0	7.4	7	54	23
First fall	31	0.2- 6.0	1.4	8	26	45	0.1-23.0	4.1	21	47	76
December to September 30 of second year	27	0.1-38.0	4.7	12	44*	23	0.2-18.0	8.9	20	87*	50
October 1 of second year and later	13	1.8-15.0	4.6	10	78	14	1.0-56.0	15.1	12	86	27

§Moved 1.6 miles or more.
†Both were orphaned, one in April and the other in July.
*Difference between females and males significant ($P < 0.01$).

Table 4. Mean Distance Moved By Adult Red Foxes Between Time of Tagging and Rehandling

Interval	Female					Male					Total rehandled
	Number rehandled	Distance moved (miles)		Dispersed*		Number rehandled	Distance moved (miles)		Dispersed*		
		Range	Mean	Number	Per cent		Range	Mean	Number	Per cent	
First spring or summer	5	0.1-0.3	0.16	0	. .	2	0.1	0.1	0	. .	7
First October through second September	10	0.1-2.2	0.94	1	10	8	0.1-2.2	0.91	1	13	18
Second October and later	5	0.6-2.5	1.46	2	40	1	1.5	1.5	0	. .	6

*Moved 1.6 miles or more.

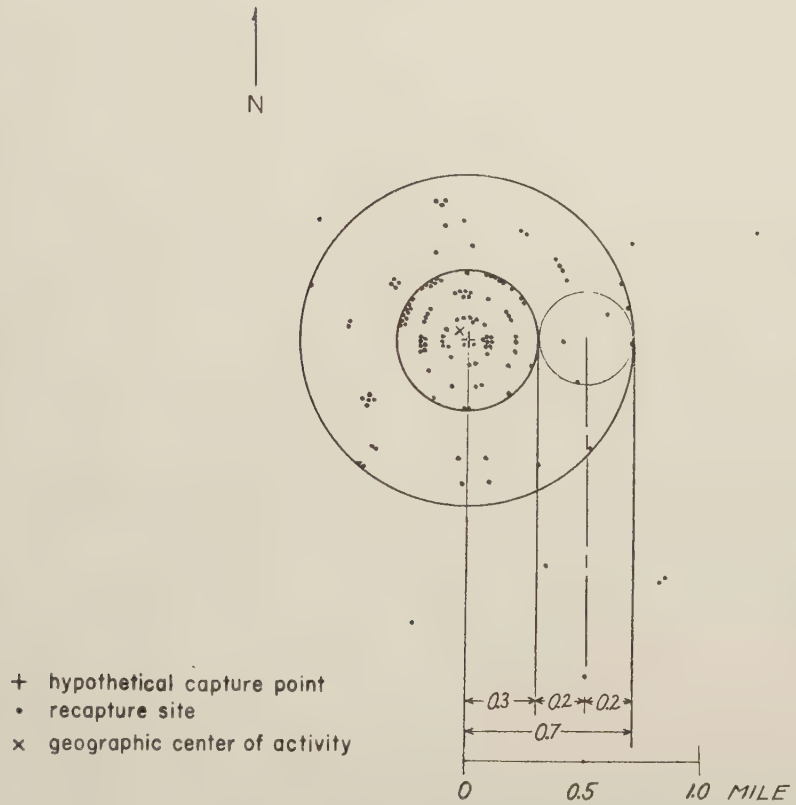


Figure 3. Summer movement of tagged red fox pups on or near the study area, as indicated by recapture sites plotted with reference to a hypothetical common original capture point. Circles represent various cruising radii as described in text.

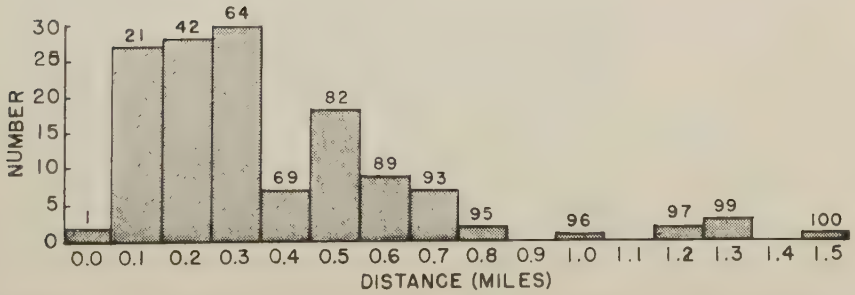
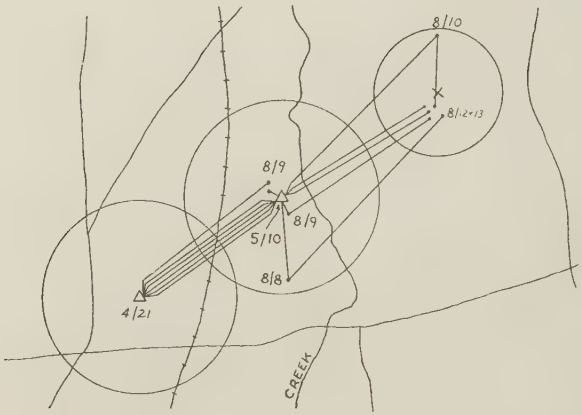
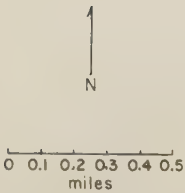


Figure 4. Frequency distribution of distances between original capture points (den or trap site) and subsequent captures for tagged red fox pups rehandled prior to October on or near the study area. Numbers over columns of graph represent cumulative percentage.



△ den site

× geographic center of activity



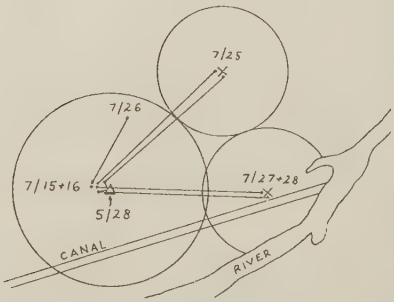


Figure 5. Diagram of recaptures of numbers of two red fox families during one spring and summer. Large circles represent 0.3-mile cruising radius of pups around den site. Small circles represent 0.2-mile cruising radius for pups after establishing independent activity centers.

Above: Two large pups dug from a den and four smaller ones (orphans) were tagged and released at that den on April 21. The four orphans, one large tagged pup and two large untagged pups were dug from a second den on May 10, the latter being tagged at that time. On August 8 and 9, four of the tagged pups were trapped near the second den, and four plus another that had not been tagged were captured 0.6 mile to the northeast from August 10 to 13. Two of the latter had been captured 3 to 5 days previously near the second den.

Below: Two of the three pups, dug from a den and tagged on May 28, were trapped near the same den with three untagged pups and an adult female on July 15 and 16. All were released with tags. No fresh fox sign was observed near the den after July 16, but sign was found to the north and east, and all of the five tagged pups handled in mid-July were recaptured from July 25 to 28. All fox sign found was located within the circles indicated.

spring. Storm (1965) reported that the average distance between day-resting and night-activity areas of a red fox pup that was radio tracked

during the summer varied from 0 to 0.23 mile. The latter range of distances was similar to that for pups in the present study.

The summer home ranges of three red fox families in Iowa, studied by Scott (1943), varied from 1.0 to 1.14 square miles. In the present study, 64 per cent of the tagged pups rehandled in their first summer had moved 0.3 mile or less (Figure 4). Considered as a cruising radius, this implied home ranges of not more than 0.28 square mile. An additional 29 per cent of these pups had traveled between 0.4 and 0.7 mile which implied home ranges as large as 1.54 square miles. Since these greater distances appeared more likely to have been the result of changes in activity centers than of increases in cruising radii, it seems probable that the home ranges of most pups were 0.28 square mile or less.

The size of the home ranges of adults was not clearly indicated by the present study. Summer home ranges of pups were, in theory, within those of their dams. The data, therefore, imply that some adult females may have had home ranges as large as 1.54 square miles. However, none of the distances recorded for seven adults that were rehandled during the same summer in which they had been trapped were long enough to suggest such a large home range. Ables (1969) estimated the summer home ranges of five adult female red foxes in Wisconsin to be from 0.27 to 0.75 square mile.

INTRASPECIFIC TOLERANCE

In the course of den excavation and summer trapping during the present study, 22 observations indicating possible intraspecific tolerance were recorded (Table 5). These included four cases of communal denning (involving 55 red foxes) and the capture of 18 members of identifiable families in each of which instances the animal was within 0.7 mile of the capture points of members of families other than its own during the same period. Sheldon (1950) concluded that red foxes were gregarious during the denning season. His evidence included eight communal red fox dens, a concentration of five red fox litters on 200 acres and several instances of pups being fostered by vixens other than their own dam. Burrows (1968) similarly interpreted observations of red foxes in England as indications of intraspecific tolerance.

Communal dens are relatively difficult to demonstrate because proof is limited to positive evidence of cooccupation by an unusually large number of pups (i.e., nine or more) or by pups of conspicuously different sizes, or of two lactating females in the same burrow system. Nevertheless, a number of instances of communal denning have been reported in addition to those noted by Sheldon (1950). Pils and Martin (1978) found five communal dens in Wisconsin, while Rue (1969) observed three in Pennsylvania and New Jersey, and Storm et al. (1976) found nine in Iowa and Illinois. Switzenberg (1950) and Holcomb (1964) both reported large red fox litters

Table 5. Instances of Intraspecific Tolerance Observed Among Red Foxes On or Near the Study Area

Year	Degree*	Section§	Foxes involved			
			Adult			
			Female	Male	Pup	Total
1972	III	D-2	1	2	1	4
1973	III	A-4	2	. .	6	8
	IV	E-8 and E-9	2	. .	6	8
	V	F-6 and G-7	. .	. .	10	10
1974	I	J-9	. .	. .	12	12
	I	†	2	2	8	12
	III	A-4	. .	. .	10	10
	III	C-1	. .	. .	12	12
	III	†	. .	2	1	3
	IV	B-3	. .	1	9	10
1975	I	A-3	2	1	14	17
	II	F-3	2	. .	4	6
	II	C-7	2	. .	11	13
	IV	J-8	1	. .	15	16
	IV	A-4	1	. .	11	12
	IV	E-4	2	2	12	16
	V	B-5 and C-5	2	. .	9	11
1976	II	†	1	3	2	6
	IV	A-2 and B-2	2	1	. .	3
	V	B-4 and C-5	. .	. .	10	10
1977	I	D-5	1	. .	13	14
	II	†	1	2	1	4
Total			24	16	177	217

Total according to degree

Degree*	Instances	Female	Male	Pup	Total
I	4	5	3	47	55
II	4	6	5	18	29
III	5	3	4	30	37
IV	6	8	4	53	65
V	3	2	. .	29	31
Total	22	24	16	177	217

* I Groups of foxes sharing same den site.
II Groups of foxes trapped within 250 feet of each other.
III Groups of foxes trapped between 0.1 and 0.3 mile of each other.
IV Groups of foxes trapped between 0.4 and 0.5 mile of each other.
V Groups of foxes trapped between 0.6 and 0.7 mile of each other.

§Location where observation was made; sections designated as described in text and illustrated in Figure 2.

†Location just off study area.

in Michigan that probably represented communal dens. Richards and Hine (1953) reported three cases in which red fox families, after the loss of both parents, moved into dens with other families. Tullar et al. (1976) observed the adoption of two entire litters in addition to the communal dens noted in Table 5. Preston (1975) studied the interactions of pairs of adult red foxes with male intruders in a large pen during the summer and

concluded that resident adult females seldom interacted with male intruders and that resident males were not dominant in most encounters. Ables (1969), in contrast, reported that the movement of two radio-tracked adult vixens suggested "territorial behavior". Sargeant (1972) followed 32 radio-tagged red foxes in Minnesota and observed that individual families occupied "well-defined, non-overlapping, contiguous territories".

The findings of the present study and those of Ables and Sargeant are not necessarily in conflict. Many of the red fox families identified on the Cayuga County area were relatively isolated and probably shared no portion of their home ranges with members of other families. However, it is important to recognize that the various reports of intraspecific tolerance constitute widespread evidence that, at times, adult red foxes and their pups do share ranges and even dens with other families during or shortly after the denning season. Ables (1969) also described the areas occupied by three radio-tagged vixens in 1965 and concluded that one of them shared about 42 per cent of her range with her tagged sibling and about 13 per cent with another adult female (relationship not specified). While Sargeant (1972) implied exclusive family use of "territories", Sargeant et al. (1975) stated that "several times pups of obvious age differences were observed together at dens" and suggested that this indicated communal denning.

Lloyd (1975) observed that "the onset of the breeding season" was a "reason for social interaction and competition" among groups of red foxes in England. Similarly, Burrows (1968) concluded that social interaction among vixens led to the establishment of "very loose communities" around a suitable number of "breeding earths" used for whelping and rearing pups until June. While breeding and whelping require intraspecific tolerance and cooperation, locally plentiful supplies of food have also been found to cause red foxes to congregate and interact socially. Phillips (1971) penned 25 red foxes (one adult female, two adult males and 22 pups) in a 13-acre enclosure and concluded that the group could live together with "little or no social strife if an adequate food supply is available". Storm (1965) and Ables (1969) both cited examples of locally abundant food holding foxes in given areas. Vincent (1958) observed the development of a social "hierarchy" among 13 individual red foxes attracted to food from November through February. Kenneth Tullar (personal conversation) observed as many as 10 red foxes feeding on the carcass of a Kodiak brown bear in November. Fisher (1951) suggested a density of 60 red foxes per square mile in plowed wheat stubble in July. In the present study, newly mown hayfields, recently harvested small grain stubble and the complete development of shade over the rows in cornfields were often found to attract red fox pups in July and August.

The interrelationship between the number of sections on the study area

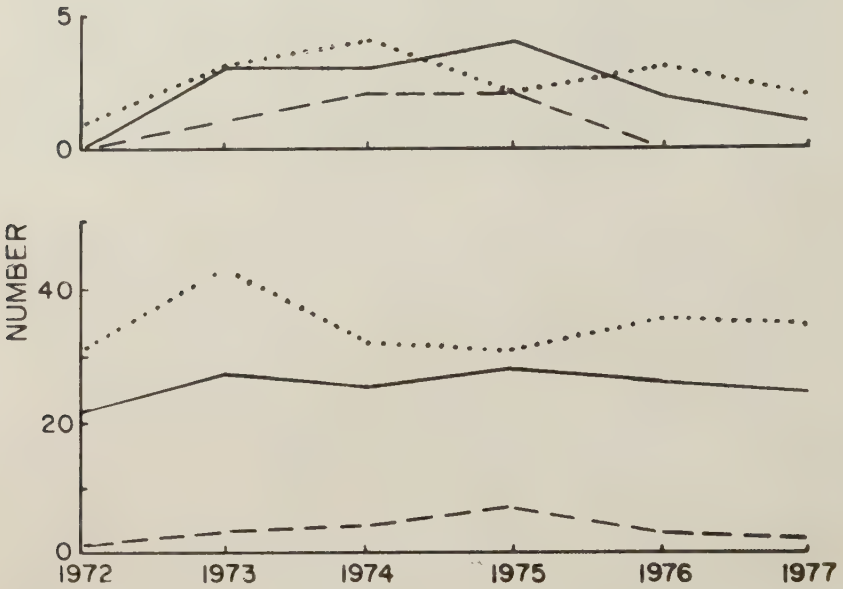


Figure 6. Interrelationships between number of occupied sections (dotted line), red fox families present (solid line) and observed cases of intraspecific tolerance (dash line) for the four most frequently occupied adjacent sections (above) and the entire study area (below). Data from Figure 2 and Table 5.

that were occupied by red foxes, the number of fox families present and the observed cases of intraspecific tolerance are shown in Figure 6. The relative change in the number of families each year appeared to be inversely related to the size of the area involved. On the four most frequently occupied adjacent sections the number of families varied from zero to four, while on the entire 100 sections the highest number (28) was only 1.33 times the lowest (21). Suitable habitat did not appear to have been a factor with respect to the intraspecific tolerance observed. If intolerance had influenced the amount of habitat used, the number of sections that were occupied, as well as the number of den sites used, would have increased when the number of families increased. However, red foxes used one section less in 1975 when the population was highest than in 1972 when the population was lowest. During the six years of the study, red foxes occupied 79 of the 100 sections, but the maximum number occupied in any one year was only 43. This indicates that the availability of suitable habitat was not a factor in inducing the intraspecific tolerance observed. In fact, as noted in connection with spring and summer distribution, in five of the six years the incidence of two red fox families sharing the same square mile of the study area suggested a tendency to accept close neighbors but to avoid concurrent home ranges.

FALL MOVEMENT

Sheldon (1950) used "dispersal" to describe the act of a juvenile leaving its parental home range to find a range of its own. Storm et al. (1976) added the concept of respacing individuals within occupied range. Behavior noted during the present study is best described as a combination of these concepts. Although the distances differ, dispersal applies to both pups and adults. Sheldon (1950), Phillips et al. (1972), Jensen (1973) and Storm et al. (1976) all indicated that dispersal movements began during October and took place gradually during the fall. Observations during the present study conformed to that pattern.

For pups, Jensen (1973) chose a movement exceeding 5 kilometers (3.1 miles) as indicating dispersal because 35 (97 per cent) of 36 tagged red fox pups, recovered before their first October, had not moved farther than that. Although several red fox pups they recovered had travelled more than 5 miles before October, Storm et al. (1976) arbitrarily chose 5 miles as the distance indicating dispersal. In the present study, 1.5 miles was chosen as the threshold distance because none of the 137 pups rehandled before their first October had travelled farther (Table 6).

Storm et al. (1976) considered increased gonadotrophic activity, inherent tendency, parental pressure and population density as possible causes of pup dispersal. They castrated a number of male pups to test the effect of inhibiting gonadotrophic activity and found that 44 per cent of them dispersed, while 80 and 37 per cent of the unaltered males and females, respectively, dispersed. They interpreted this as indicating that gonadotrophic activity only partly influenced dispersal. The intensive effort to capture red foxes during the present study afforded an opportunity to test the influence of local population density on pup dispersal rates. Based on captures known to have included all pups within 0.7 mile of

TABLE 6. DISTANCE MOVED BY TAGGED RED FOXES REHANDLED AFTER OCTOBER, ACCORDING TO AGE AND SEX

Age and sex	Number	Distance moved (miles)§					
		0-1.5	1.6-4.9	5.0-9.9	10-19.9	20-29.9	30 or more
Juvenile							
Male	82	29 (35)*	12 (15)	17 (21)	19 (23)	2 (2)	3 (4)
Female	73	43 (59)*	15 (20)	9 (13)	5 (7)	. . . .	1 (1)
Sub-total	155	72 (46)	27 (17)	26 (17)	24 (16)	2 (1)	4 (3)
Adult							
Male	9	8 (89)	1 (11)	. . . .	. . . .	. . . .	. . . .
Female	15	12 (80)	3 (20)	. . . .	. . . .	. . . .	. . . .
Sub-total	24	20 (83)	4 (17)	. . . .	. . . .	. . . .	. . . .
Total	179	92 (51)	31 (17)	26 (15)	24 (14)	2 (1)	4 (2)

§Figures in parentheses represent percentages.
*Difference significant ($P < 0.01$).

Table 7. Relationship of Group Size (i.e., Population Density) to Dispersal For 94 Red Fox Pups Rehandled Between Their First September and Second October§

Sex	Group size†	Number rehandled	Dispersed	
			Number	Per cent
Male	Small	34	20	59
	Large	20	12	60
Total		54	32	59
Female	Small	25	6	24**
	Large	15	8	53
Total		40	14	35

§Represents initial captures known to have included all pups within 0.7 mile of others during the same spring and summer.

†Small = 1 to 5 pups; large = 6 to 15 pups.

**Difference between females from small groups and males from groups of either size highly significant ($P < 0.01$).

others on the study area, small groups (1-5, i.e., low density) and large groups (6-15, i.e., higher density) were differentiated (Table 7). For 94 of these pups that were rehandled after their first September and before their second October, 46 (48 per cent) had travelled 1.6 miles or more. Among the small groups, significantly more ($P < 0.01$) males than females dispersed (59 vs. 24 per cent, respectively). However, among the large groups, 53 per cent of the females dispersed which was not significantly different from the rate for males from groups of either size. Thus it appeared that comparatively high local densities of pups may have increased the tendency of female pups to disperse but did not affect the dispersal of male pups which was basically quite high.

Jensen (1973) reported that among tagged red fox pups, recovered from November through February of their first year, 81 per cent of the males and 24 per cent of the females had dispersed (i.e., moved 3.1 miles or more). Storm et al. (1976) reported that 87 and 37 per cent, respectively, of male and female pups recovered from October through March of their first year had dispersed (i.e., moved 5 miles or more). For all records in the present study, 87 and 44 per cent of the male and female pups, respectively, recovered from November through their second October, had dispersed (i.e., moved 1.6 miles or more). Considering the differences in threshold distance, there is surprisingly close agreement in the dispersal rates observed in these three studies.

European workers found that comparatively few juvenile red foxes travelled more than 50 kilometers (31 miles). Marcstrom (1968) in Sweden and Jensen (1973) in Denmark found that 8 per cent and 2.6 per cent, respectively, of red fox pups had travelled that far. In Iowa and Illinois, in contrast, Storm et al. (1976) found that of 504 tagged pups, recovered from October through March of their first year, 19 per cent had dispersed

30 miles and 3.8 per cent had travelled more than 60 miles. The findings of the present study are closer to those from Europe. Only 3 per cent of 153 pups rehandled after October had travelled 30 miles or more, and none had travelled as far as 60 miles (Table 6). The longest distance travelled by any of the red foxes tagged in central New York by Sheldon (1950) was 40 miles. The distances reported for tagged pups in New York and Europe are considerably less than the 245 miles travelled by a pup in Wisconsin (Ables, 1965), the 169 miles travelled by one in Michigan (Arnold and Schofield, 1956) or the 130 and 215 miles travelled by two males and 159 miles by a female as reported by Storm et al. (1976).

The average distance travelled by dispersing pups in the present study suggests that neither the habitat nor the population density in Cayuga County required dispersing pups to travel as far as pups in the Midwest where cover is less diversified and relative population densities may have been higher. Lloyd (1975), reporting on the movements of 272 tagged red fox pups in the United Kingdom, indicated that the mean distances travelled by males and females recovered from September through December were 2.9 and 1.2 miles, respectively, in west-Wales, but 6.5 and 1.4 miles, respectively, in mid-Wales. West-Wales was described as being very good fox habitat with much cover interspersion, many small fields and exceptionally numerous red foxes. Mid-Wales, in contrast, was described as "predominantly sheep rearing, hill areas" with large pastures and less cover diversity where fox densities were "low to moderate". Storm et al. (1976), in Illinois and Iowa where unbroken fields are often much larger than those in Wales or central New York, found that the mean distances travelled by male and female red fox pups recovered from September through December were 19.6 and 5.8 miles, respectively. In the present study, the corresponding figures were 3.5 and 1.9 miles, respectively. This suggests that the red fox habitat in Cayuga County is similar in value to that of Wales. However, the densities of red fox families reported by Sargeant et al. (1975) for North Dakota are not greatly different from those observed in the present study. Regions with greater habitat diversity would be expected to have greater numbers of potential red fox home ranges per unit area than regions, such as the northcentral United States, with less habitat diversity. At the same time, areas with high diversity often support high fox population densities, so that the tendency of pups to disperse long distances may not be related to density, *per se*, so much as to the relative population level with respect to the number of potential home ranges per unit area. Therefore, it would appear that the study area in Cayuga County was understocked with red fox families and that the pups usually did not have to travel very far to establish their own home ranges.

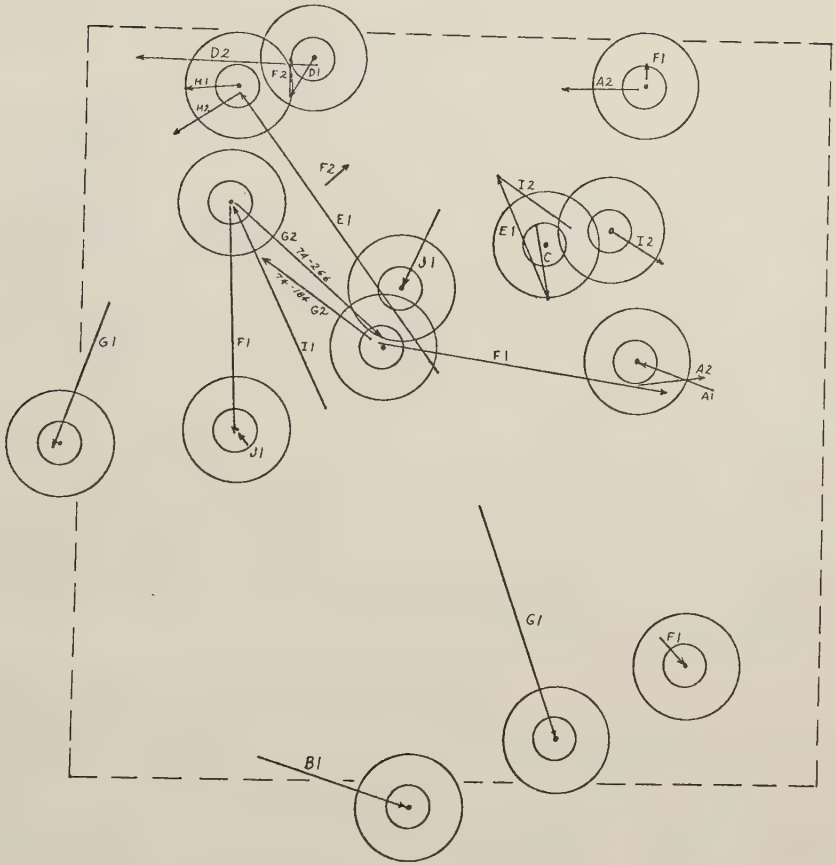
Sheldon (1950) observed that "a trap set on a good fox runway often takes 25 to 30 animals during six weeks in the fall". Korschgen (1959) reported a catch of 22 red foxes in a single trap during the fall. Such

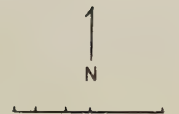
reports are not unusual, and most experienced fox trappers are very careful to record the locations of successful "sets". Fox tracking during the present study indicated that red foxes usually followed fencerows, farm lanes, field edges and other linear terrain features. Dispersing young foxes may also follow such linear features rather than take random courses. In considering the possibilities for "social contacts" between dispersing and resident red foxes, Storm and Montgomery (1975) assumed that both animals moved at random in the home range of the resident. However, this assumption is not consistent with experience during the present study, and it seems more likely that both residents and dispersing animals follow some of the linear features. Such travel would greatly increase the probability of transients finding the scent or caches of residents, and it may also be the way in which dispersing animals find "open" home ranges. This hypothesis would also explain why so many red foxes can sometimes be captured in the same set in a relatively short period of time.

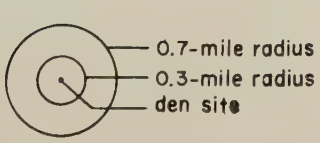
Travel Patterns and Distances of Adult Foxes

Jensen (1973) reported that a female red fox in Denmark, tagged as an adult, had moved 11 kilometers (6.8 miles), but he expressed the opinion that adults usually did not move far once they had reproduced. Storm et al. (1976), in contrast, reported that 30 and 21 per cent, respectively, of male and female red foxes tagged as adults in the northcentral United States had moved 5 miles or more.

The movement of adult female red foxes tagged on the study area, in relation to known denning sites, is shown in Figure 7. Even though 2.5 miles was the greatest distance that any of these vixens had moved, eight of nine that were rehandled after 10 months had moved away from their old denning territories. In one case, two adult vixens (74-184 and 74-266) handled at their dens in 1974 had apparently swapped den sites (a movement of more than 1.5 miles) when rehandled in 1976. Table 3 shows that among 13 vixens, tagged as pups and rehandled during or after their second autumn, 10 (78 per cent) had dispersed (moved at least 1.6 miles). This was not significantly different from the corresponding proportion for males, i.e., 12 (86 per cent) of 14. However, of 27 vixens that were rehandled during or after their first autumn only 12 (44 per cent) had dispersed, which was a significantly ($P < 0.01$) lower proportion than the 20 (87 per cent) of 23 males for the same period. Thus, while the movement of females was somewhat limited, most of those surviving apparently modified or left earlier home ranges before each whelping season, and the cumulative effect of these short movements was a dispersal rate similar to that of males. The comparatively short distances moved by such vixens probably reflects the "richness" (many choices) of the study area in terms of den sites or year to year shifts in prey availability.







SYMBOL	YEARS HANDLED
A	1972 & 1973
B	1972 & 1974
C	1973 - 1973
D	1973 & 1974
E	1973 & 1975
F	1974 & 1975
G	1974 & 1976
H	1975 & 1976
I	1975 & 1977
J	1976 & 1977

1 pup at first capture
2 adult at both handlings

Figure 7. Points of 20 initial captures and 24 rehandlings of adult female red foxes plotted with reference to den sites. Arrows indicate distance and direction of movement in each case. Boundary of study area shown by dash line.

Effects of Sarcoptic Mange Upon Movement

Infestations of sarcoptic mange were found on 17 pups that were rehandled from 2 to 8 months after being tagged. Two had succumbed to mange alone and a third was killed by a dog because of its weakened condition. The other 14 were trapped, shot or killed by cars and had mange infestations that would not have immediately resulted in death. Stone et al. (1972) reported that, in experimental infestations of red foxes, sarcoptic mange caused increasing stress and discomfort in from 1 to 2 months and death in 2 to 4 months. In the present study, none of 10 pups rehandled and found mangy during the summer in which they were tagged had moved an unusual distance. Of seven pups, rehandled and found mangy during their first fall, none had dispersed, while of 83 non-mangy pups rehandled during the same period 38 (46 per cent) had dispersed. If mange had not affected their will or ability to travel, at least three "dispersers" would have been expected among the seven mangy pups. It seems probable that good health is required for a juvenile fox to leave familiar habitat.

Sarcoptic mange was also found on 10 (34 per cent) of 29 red foxes that were tagged as adults and rehandled from 2 to 30 months after being tagged. None of the mangy adults had moved even though four (21 per cent) of 19 rehandled non-mangy adults had moved between 1.6 and 2.5 miles. Therefore, at least two "dispersers" would have been expected among the 10 mangy adults if mange had not inhibited their will or ability to travel.

CONCLUSIONS

The data gathered on the study area in Cayuga County indicate that, on range such as that in central New York, sections on the order of a square mile in size are seldom occupied concurrently by more than one adult female red fox and her family, but families may be tolerated on adjacent sections at about the frequency that would occur at random. At the same time, some communal denning and range sharing also occur. Intraspecific tolerance is apparently not influenced by either population density or the amount of suitable habitat. The number of adult females in an area tends to be relatively stable, while annual fluctuations in the over-all population level are greater.

The majority of red fox pups travel within a radius of 0.3 mile and occupy home ranges of 0.28 square mile or less during their first summer. Movements greater than that appear to represent changes in the center of activity for the pups involved. The summer ranges of some adults may have been as large as 1.54 square miles. Dispersal movements begin in October and take place gradually during the fall, and data indicated 1.5 miles to be the threshold distance beyond which a fox pup may be considered to have moved to a new territory. The distance to which pups disperse may be related primarily to the relative population level with respect to the

number of potential home ranges per unit area. After their first breeding season adults did not travel far, but females usually chose new den sites in subsequent years. Infestations of sarcoptic mange appear to inhibit dispersal of both pups and adults.

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The *New York Fish and Game Journal* is devoted to presenting the results of research and management studies in New York, and other technical papers on related subjects, that pertain to fish and wildlife problems of concern to the Department of Environmental Conservation. It is published semi-annually and is distributed free to official conservation agencies and scientific organizations in New York State. Others may subscribe at a rate of $1.50 per year or obtain individual issues for 75¢ per copy. Correspondence should be addressed to the Editor Robert W. Darrow, New York State Department of Environmental Conservation, Wildlife Resources Center, Delmar, N.Y. 12054.

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